CHAPTER 5:
PATTERNS OF BIRD DIVERSITY

RESULTS

Patterns of Bird Alpha Diversity

General Patterns

A total of 101 species of birds were detected on sample reaches (Appendix 7). Bird species richness based on point count and riparian search data ranged from 16 to 49 ($\bar{x}$ = 35.3, SE = 0.80) species per reach. Sampling detected approximately 70% of the 149 species known to regularly occur in the Lake Tahoe basin. The species not detected consisted primarily (57%) of species associated with standing water (i.e., waterfowl, herons, terns, rails), including the Bald Eagle (*Haliaeetus leucocephalus*) (Appendix 19). Three additional species not detected were seasonal migrants (Varied Thrush [*Ixoreus naevius*], Gray-crowned Rosy Finch [*Leucosticte tephrocotis*], Tundra Swan [*Cygnus columbianus*]), and 2 more were nocturnal (Spotted Owl [*Strix occidentalis*], Western Screech Owl [*Otus kennicottii*]). The remaining species (32%) include a diversity of species which are rarely sighted in the Lake Tahoe basin because the basin provides little suitable habitat for them. These results suggest that sampling detected the majority of species associated with stream-side riparian environments in the basin. Four species not considered regularly occurring were observed: Black-chinned Hummingbird (*Archilochus alexandri*), Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), Black-throated Gray Warbler (*Dendroica nigrescens*), and Bewick's Wren (*Thryomanes bewickii*).

The 10 most frequently occurring species (Fig. 16) were responsible for approximately 38% of all observations. The 10 most frequent species were all forest associates. Five species occurred on every reach: Yellow-rumped Warbler (*Dendroica coronata*), Steller's Jay (*Cyanocitta stelleri*), Dark-eyed Junco (*Junco hyemalis*), Mountain Chickadee (*Poecile gambeli*), and American Robin (*Turdus migratorius*).

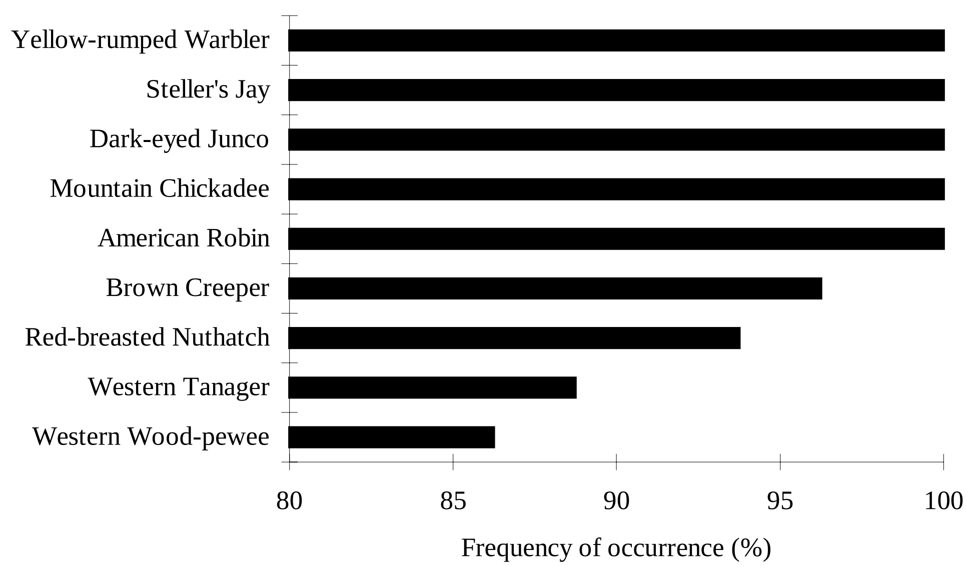

FIG. 16. Ten most frequently occurring bird species. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of Species Richness

Correlations

Bird species richness was correlated with 10 environmental variables (Table 38). Relative to physical features, negative correlations were observed with elevation, precipitation, and channel gradient, and a positive correlation was observed with sinuosity. Bird species richness declined in association with subalpine conifer, and increased with increases in aspen–cottonwood, to lodgepole pine, and meadow.

Regression Model for Bird Species Richness

Regression models closely reflected correlations with environmental variables and showed moderately strong relationships (Table 39). Regression on abiotic environmental variables resulted in a 2-variable model: a negative association with elevation and precipitation (adj. R^2 = 0.153). Regression on channel variables resulted in a 2-variable model: negative associations with channel gradient and channel width (adj. R^2 = 0.219). Regression on vegetation variables resulted in a 2-variable model: a positive association with meadow, and a negative association with subalpine conifer (adj. R^2 = 0.279). Backwards step-wise regression on these 6 key variables resulted in a final 3-variable model, with a bird species richness increasing with an increasing proportion of meadow and a decrease in precipitation and channel gradient (adj. R^2 = 0.325) (Tables 39 and 40).

TABLE 38. Environmental variables correlated ($P \leq 0.10$) with bird species richness. Bolded values indicate $P \leq 0.05$. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	r	*P*
Abiotic environment:		
Elevation	**-0.313**	**0.005**
Precipitation	**-0.337**	**0.002**
Channel characteristics:		
Gradient	**-0.376**	**0.001**
Sinuosity	0.199	0.077
Vegetation characteristics:		
Subalpine conifer	**-0.304**	**0.006**
Lodgepole pine	**0.233**	**0.038**
Aspen–cottonwood	0.191	0.089
Meadow	**0.477**	**<0.001**
Small log	-0.210	0.062
Large log	-0.212	0.059

TABLE 39. Variables selected in step-wise regressions between 3 groups of environmental variables (*n* = 22) and bird species richness. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Bird species richness
Abiotic environment:	
Elevation	N
Precipitation	**N**
Channel characteristics:	
Gradient	**N**
Width	N
Vegetation characteristics:	
Meadow	**P**
Subalpine conifer	N
Variables in final model	*3*
adj. R^2	*0.325*

TABLE 40. Final regression model of key environmental variables related to bird species richness at sample reaches (*n* = 80) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Precipitation	-6.727	2.038	-0.314	-3.302	0.002
Meadow	7.240	2.521	0.308	2.872	0.005
Channel gradient	-2.609	1.065	-0.261	-2.449	0.017

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with precipitation in the basin (r = -0.353, *P* = 0.001). It is possible that the negative relationship observed between bird species richness and precipitation is a consequence of disturbance being higher in areas with lower precipitation. An analysis of covariance with precipitation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that bird species richness did not vary significantly among precipitation classes, nor was it correlated with meso-scale disturbance (adj. R^2 = 0.018) (Table 41). ANOVA between bird species richness and precipitation (without meso-scale disturbance as a covariate) was also not significant (r = 1.74, *P* = 0.166). This indicates that precipitation was not a strong predictor of bird species richness, and that this relationship was not influenced by disturbance.

TABLE 41. Analysis of covariance exploring the relationship between bird species richness and precipitation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

Source of variation	ν	SS	MS	F	*P*
Within + residual	75	3800.21	50.67		
Regression	1	15.19	15.19	0.30	0.586
Precipitation	3	273.51	91.17	1.80	0.155
Model	4	277.34	69.33	1.37	0.253
Total	79	4077.55	51.61		

I looked for potential thresholds in bird species richness in relation to the 3 primary environmental variables associated with variation in richness (precipitation, channel gradient, and meadow). All of the relationships were linear, with the exception of the relationship between bird species richness and meadow. It appeared that richness was lowest when meadow comprised < 10% of the sample area, was moderate when meadow comprised 10 to 30% of the sample area, and was consistently high where meadow comprised > 30% of the sample area (Fig. 17). Bird species richness was significantly greater where meadow comprised an excess of 10% of the sample reach (1-tailed test, pooled variance, $t = 4.65$, $P < 0.001$).

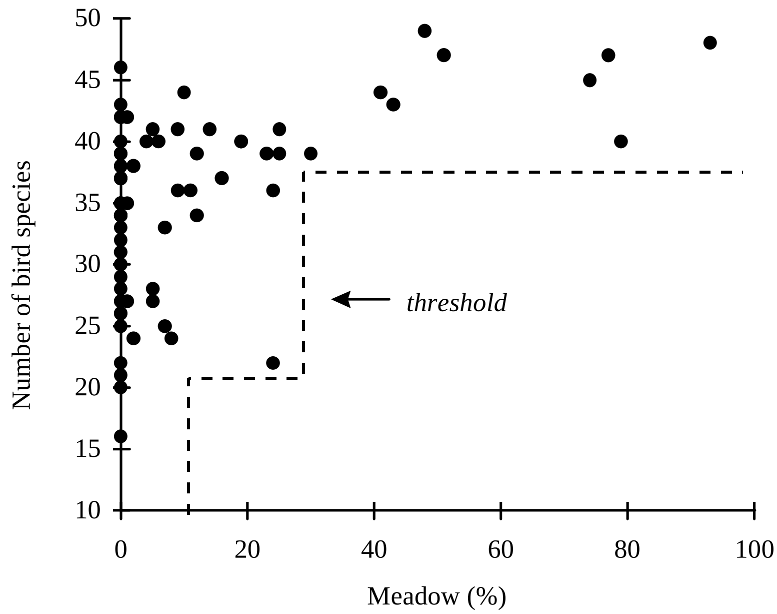

FIG. 17. Threshold between bird species richness and meadow. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Bird Species Richness by Environmental Gradients

Bird species richness was positively correlated with the forest to meadow and aspen–cottonwood gradients, and negatively correlated with the elevation–precipitation and snag and log gradients (Table 42).

Bird Species Richness by Basin Orientation

Bird species richness varied significantly among basin orientations ($\nu = 3, 76$; SS = 797.72, 3045.97; MS = 265.91, 40.08; F = 6.635; $P < 0.001$). Bird species richness was greater on the east side compared to the north and west sides of the basin based on Tukey's test ($P < 0.05$).

Environmental Relationships of Bird Abundance

The total abundance of birds per point count on each reach ranged from 4.4 to 26.5 individuals ($\bar{x} = 12.8$, SE = 0.50). Bird species richness and abundance were highly correlated ($r = 0.752$, $P < 0.001$), with abundance increasing with increases in richness (Fig. 18).

TABLE 42. Correlations between bird species richness and environmental gradients based on principal component analysis. Bolded values indicate $P \leq 0.10$. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradients	Bird species richness r	*P*
Physical gradients:		
1. Elevation–precipitation	**-0.393**	**<0.001**
2. Channel flow	0.145	0.200
Vegetation gradients:		
1. Forest to meadow	**0.402**	**<0.001**
2. Subalpine vegetation	-0.151	0.181
3. Alder–willow	0.028	0.803
4. Aspen–cottonwood	**0.325**	**0.003**
Woody debris gradients:		
1. Snag and log	**-0.204**	**0.069**

The most abundant species will make the greatest contribution to total abundance, and environmental relationships of bird abundance will reflect their (abundant species) associations to a greater degree. The 10 most abundant bird species were Mountain Chickadee, Steller's Jay, Dark-eyed Junco, Yellow-rumped Warbler, American Robin, Warbling Vireo, Fox Sparrow (*Passerella iliaca*), Red-breasted Nuthatch (*Sitta canadensis*), Western Wood-pewee (*Contopus sordidulus*), and Pine Siskin (*Carduelis pinus*) (Fig. 19). The 3 most abundant species comprised an average of over 50% of all birds detected. The 3 most abundant species had similar abundances, with the remaining 7 species having significantly lower abundance. Mountain Chickadee was not significantly more abundant than the Steller's Jay ($P = 0.156$, pooled variance), and Steller's Jay was not significantly more abundant than Dark-eyed Junco ($P = 0.7180$, pooled variance). However, Dark-eyed Junco was significantly more abundant than Yellow-rumped Warbler ($\nu = 150$, $t = 9.240$, $P < 0.001$). No other sequential species comparisons of abundance were significantly different for the 10 most abundant bird species.

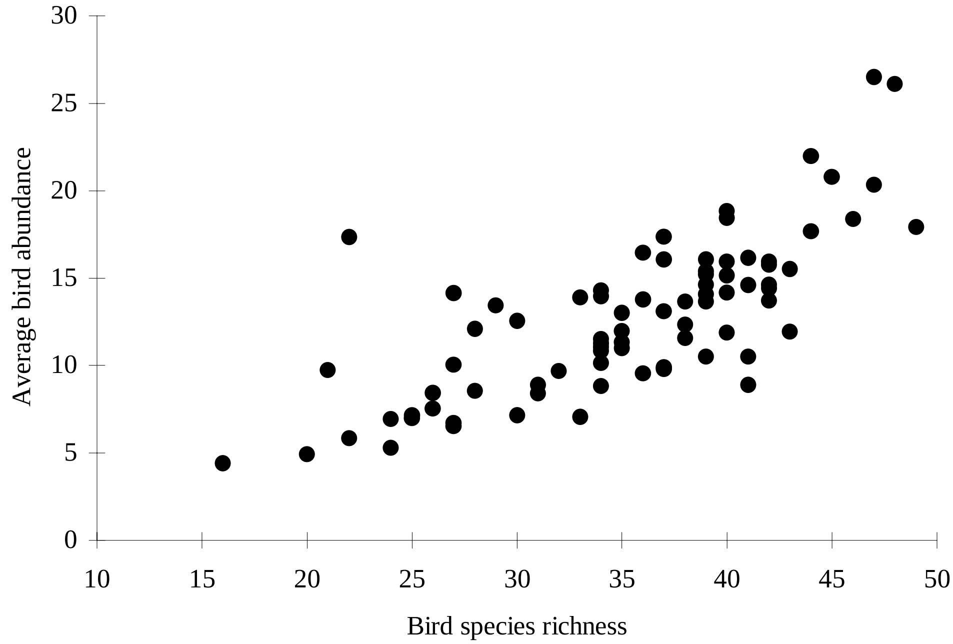

FIG. 18. Total bird species richness relative to average abundance per point count on 80 stream reaches in the Lake Tahoe basin, 1995 to 1996.

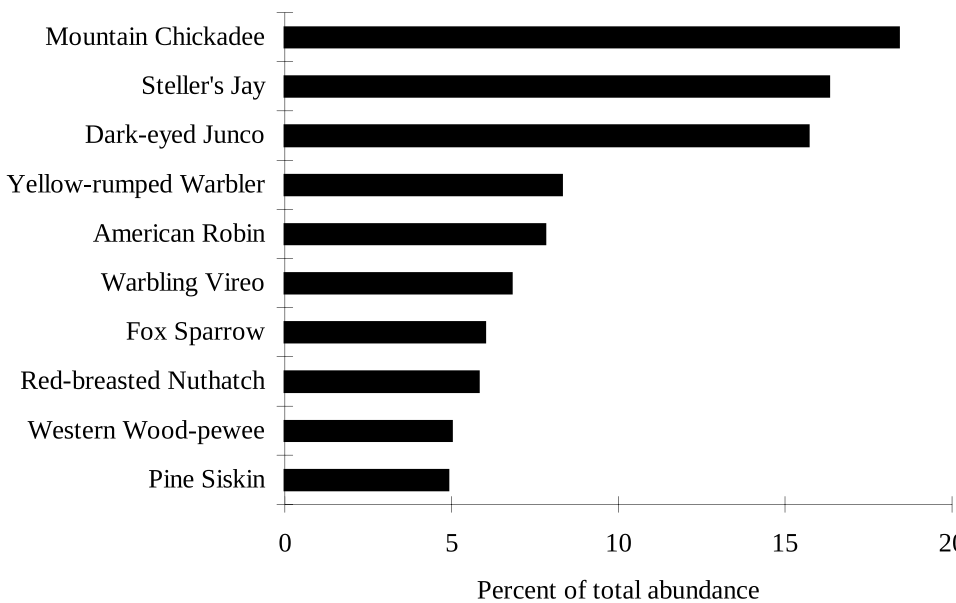

FIG. 19. Ten most abundant bird species and their contributions to total bird abundance on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Regression Model for Bird Abundance

Thirteen environmental variables were correlated with bird abundance (Table 43). Regression models closely reflected correlations with environmental variables, were very similar to models for richness, and showed moderately strong relationships (Table 44). Regression on abiotic environmental variables resulted in a 2-variable model: negative associations with elevation and precipitation (adj. $R^2 = 0.180$). Regression on channel variables resulted in a 2-variable model: negative associations with channel gradient and channel width (adj. $R^2 = 0.297$). Regression on vegetation variables resulted in a 3-variable model: a positive association with meadow; and negative associations with subalpine conifer and small snags (adj. $R^2 = 0.464$). Backwards step-wise regression on these 7 key variables resulted in a 3-variable model, with bird abundance increasing with increasing meadow and decreasing elevation and channel width (adj. $R^2 = 0.520$) (Tables 44 and 45).

TABLE 43. Environmental variables correlated ($P \leq 0.10$) with bird abundance. Bolded values indicate $P \leq 0.05$. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	r	*P*
Abiotic environment:		
Elevation	**-0.312**	**0.005**
Precipitation	**-0.399**	**<0.001**
Channel characteristics:		
Gradient	**-0.375**	**0.001**
Sinuosity	0.196	0.081
Width	**-0.273**	**0.014**
Vegetation characteristics:		
Mixed conifer	-0.189	0.093
Subalpine conifer	**-0.330**	**0.003**
Meadow	**0.632**	**<0.001**
Small log	**-0.459**	**<0.001**
Large log	**-0.434**	**<0.001**
Small snag	**-0.325**	**0.003**
Large snag	**-0.331**	**0.003**
Channel volume	**-0.250**	**0.025**

TABLE 44. Variables selected in step-wise regressions between 3 groups of environmental variables (*n* = 22) and bird abundance. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Bird abundance
Abiotic environment:	
Elevation	**N**
Precipitation	N
Channel characteristics:	
Gradient	N
Width	**N**
Vegetation characteristics:	
Subalpine conifer	N
Meadow	**P**
Small snags	N
Variables in final model	*3*
adj. R^2	*0.520*

TABLE 45. Final regression model of key environmental variables related to total bird abundance at sample reaches (*n* = 80) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Meadow	8.616	1.153	0.587	7.476	<0.001
Elevation	-16.959	4.486	-0.299	-3.780	<0.001
Channel width	-2.058	0.595	-0.273	-3.459	0.001

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ($r = -0.515$, $P < 0.001$). It is possible that the negative relationship observed between bird abundance and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal-sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible the observed relationship between bird abundance and elevation (adj. $R^2 = 0.140$) (Table 46).

TABLE 46. Analysis of covariance exploring the relationship between bird abundance and elevation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	1297.13	75	17.30		
Regression	7.55	1	7.55	0.44	0.511
Elevation	165.72	3	55.24	3.19	0.028
Model	291.55	4	72.89	4.21	0.004
Total	1588.68	79	20.11		

I looked for potential thresholds in bird abundance in relation to the 3 primary environmental variables associated with variation in abundance (elevation, channel width, and meadow). All of the relationships were linear, with no apparent thresholds.

Bird Abundance by Basin Orientation

Bird abundance varied significantly by basin orientation (ν = 3, 76; SS = 164.93, 1423.75; MS = 54.98, 18.73; F = 2.93; P = 0.039). Abundance was highest on the east side, followed by the south and west, with the north side of the basin having the lowest bird abundance. The east side had significantly greater bird abundance compared to the north side based on Tukey's test ($P < 0.05$).

Gradients of Bird Abundance

Of the 34 families of birds detected during sampling, 11 families had frequencies of < 10%, leaving 23 families for inclusion in the PCA analysis to identify gradients of bird abundance (Table 47). The PCA extracted 7 factors, which explained a total of 68.2% of the variation in bird family abundance among reaches. The first 4 factors explained a total of 51.4% of the variation in abundance among families (Table 47). The latter 3 factors explained less than 7% each and were the result of the conditions on a limited number of sample reaches.

Factor 1 explained 23.2 % of the variation, and represented birds that are generally associated with open water (Table 47). All families loading on this factor were positively associated, and consisted of ducks and geese (Anatadae), grosbeaks and buntings (Cardinalidae), pigeons and doves (Columbidae), blackbirds (Icteridae), and sandpipers (Scolopacidae). Most of these families are associated with water and open habitats. Factor scores were correlated with the following environmental variables: positive correlations with channel width, meadow, and lodgepole pine; and negative correlations with elevation, precipitation, channel gradient, distance from stream mouth, small and large logs, large snags, and subalpine conifer. This factor appeared to represent open-water associated species and environments with large streams with low gradients, slow water, wide flood plains, and dominated by meadow and lodgepole pine vegetation.

Factor 2 explained 13.1 % of the variation in bird community composition among reaches, and consisted of cavity-nesting birds and forest associates (Table 47). All 4 families loading on this factor were positively associated, and consisted of creepers (Certhidae), chickadees (Paridae), nuthatches (Sittadae) and woodpeckers (Picidae). Factor scores were correlated with the following environmental variables: positive correlations with canopy cover index, aspen–cottonwood, and mixed conifer; and negative correlations with precipitation, channel width, and subalpine conifer. This factor appeared to represent upland-associated species and environments with low elevation, closed canopy forests.

Factor 3 explained 10.7% of the variation in bird community composition among reaches, and represented birds associated with open forests and riparian habitats (Table 47). All 3 families loading on this factor were positively associated, and consisted of sparrows (Emberizidae), flycatchers (Tyranidae), and vireos (Vireonidae). Factor scores were correlated with the following environmental variables: positive correlations with sinuosity, alder–willow, and lodgepole pine; and negative correlations with channel gradient, canopy cover index, and mixed conifer. This factor appeared to represent aqua- associated species and environments with well developed riparian vegetation.

TABLE 47. Principal components analysis on bird family abundance. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Bird family	Common name	Principal component analysis factor scores: Factor 1	Factor 2	Factor 3	Factor 4
Icteridae	Blackbirds	**0.852**	0.126	0.197	-0.082
Anatidae	Ducks and geese	**0.789**	-0.026	0.090	-0.053
Cardinalidae	Grosbeaks and buntings	**0.702**	0.034	-0.053	-0.276
Columbidae	Pigeons and doves	**0.694**	0.463	0.028	-0.144
Scolopacidae	Sandpipers	**0.447**	-0.115	0.390	-0.045
Paridae	Chickadees	0.042	**0.756**	0.147	0.048
Sittidae	Nuthatches	0.069	**0.731**	-0.135	0.251
Certhidae	Creepers	-0.197	**0.632**	0.189	0.098
Picidae	Woodpeckers	0.345	**0.540**	0.174	-0.023
Embezeridae	Warblers and sparrows	0.017	-0.107	**0.835**	-0.030
Tyrannidae	Tyrant flycatchers	0.088	0.313	**0.773**	0.138
Vireonidae	Vireos	0.124	0.159	**0.714**	0.154
Regulidae	Kinglets	-0.316	-0.017	-0.151	**0.707**
Thraupidae	Tanagers	0.099	0.402	0.027	**0.699**
Parulidae	Wood-warblers	-0.044	0.033	0.373	**0.684**
Turdidae	Thrushes	0.329	0.118	0.128	**0.421**
Corvidae	Jays, crows, and magpies	0.262	0.380	-0.121	**-0.470**
Troglodytidae	Wrens	-0.078	-0.061	0.209	-0.126
Hirundinidae	Swallows	0.477	-0.247	-0.236	0.029
Fringillidae	Finches	0.030	-0.029	0.210	-0.007
Odontophonidae	Quail	-0.045	-0.026	0.239	-0.004
Accipitridae	Hawks and eagles	-0.003	0.074	-0.064	0.076
Trochilidae	Hummingbirds	-0.253	-0.428	0.354	-0.046
Eigen value		*4.41*	*2.49*	*2.04*	*1.59*
Variation explained (%)		*23.2*	*13.1*	*10.7*	*6.9*

Factor 4 explained 6.9 % of the variation in bird family composition among reaches, and represented cup-nesting birds, and foliage foraging birds associated with forested habitats (Table 47). Three families were most strongly associated with the factor, had positive associations, and consisted of wood-warblers (Parulidae), kinglets (Regulidae), and tanagers (Thraupidae). The other two families had weaker associations (factor scores close to scores on other factors), consisting of a positive association with thrushes (Turdidae) and a negative association with jays and crows (Corvidae). The environmental associations of this group of families were not strong. Factor scores were positively correlated with small and large snags. This factor is most likely associated with large trees, as reflected in its association with large snags. However, the size and density of live trees was not measured directly.

Factors 5, 6, and 7 explained 6.7 %, 5.7%, and 4.5 % of the total variation, respectively. They represented 1 to 2 reaches with large numbers of swallows (Hirundinidae), finches (Fringillidae), and hawks and eagles (Accipitridae), respectively. In summary, the major gradients in bird community composition were: open-water associated species, riparian-associated species, upland-associated species, and large tree and snag-associated species.

Bird Abundance Gradients in Relation to Environment Gradients

Several correlations existed between bird abundance gradients and environmental gradients (Table 48). Bird factor 1 (water and open habitat-associated birds) was positively correlated with channel flow and forest to meadow gradients, negatively correlated elevation–precipitation, subalpine vegetation, and snag and log densities. Bird factor 2 (cavity nesters and forest associates) was positively correlated with aspen–cottonwood and negatively correlated with elevation–precipitation, and the other 3 vegetation gradients (forest to meadow, subalpine vegetation, and alder–willow). Bird factor 3 (riparian associates) was positively correlated with 3 gradients, including channel flow, forest to meadow, and alder–willow. Bird factor 4 (open-cup nesting, foliage foraging forest associates) was positively correlated with one gradient, snag and log. No bird factors were correlated with woody debris factor 2.

TABLE 48. Significant correlations ($P \leq 0.10$) between bird abundance principal component analysis (PCA) factors and environmental gradient PCA factors. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Bird family abundance gradient*							
	Factor 1		Factor 2		Factor 3		Factor 4	
Environmental gradient	r	*P*	r	*P*	r	*P*	r	*P*
Physical gradient:								
1. Elevation–precipitation	**-0.439**	**<0.001**	**-0.367**	**0.001**	P	n.s.	N	n.s.
2. Channel flow	**0.373**	**0.001**	N	n.s.	0.213	0.058	N	n.s.
Vegetation gradient:								
1. Forest to meadow	**0.342**	**0.002**	-0.214	0.056	**0.456**	**<0.001**	N	n.s.
2. Subalpine vegetation	**-0.291**	**0.009**	**-0.239**	**0.033**	N	n.s.	N	n.s.
3. Alder–willow	N	n.s.	**-0.271**	**0.015**	**0.317**	**0.004**	P	n.s.
4. Aspen–cottonwood	P	n.s.	**0.245**	**0.029**	P	n.s.	P	n.s.
Woody debris gradient:								
1. Snag and log	**-0.441**	**<0.001**	P	n.s.	N	n.s.	0.217	0.053

* Factor 1 = water and open habitat-associated birds; Factor 2 = cavity nesters and forest associates; Factor 3 = riparian associates; Factor 4 = open-cup nesting, foliage foraging forest associates.

Patterns of Bird Alpha Diversity by Habitat Association

General Patterns

Patterns of bird species richness were explored in relation to association with 3 major habitat conditions: aquatic, riparian–meadow, and upland. Upland-associated and riparian-meadow–associated species occurred on every reach, whereas aqua-dependent species were present on only 50% of the reaches. An average of 27 upland-associated species were detected on each reach, over 4 times higher an average than riparian-meadow–associated, and almost 30 times more than aqua-dependent species (Table 49).

TABLE 49. Descriptive statistics for the richness of 3 bird groups base on habitat associations. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Bird group	Total species possible	Freq. (%)	Minimum	Maximum	Ave.	SE
Aqua-dependent	11	50	0	7	1.0	0.16
Riparian-meadow–associated	28	100	1	13	6.6	0.30
Upland-associated	61	100	14	37	27.3	0.55

The contribution of individual bird species to species richness values for each group can be substantially different among species. I looked at the contribution of individual bird species to the richness of each habitat group. In the aqua-dependent group, mallards were over twice as frequent as the next most frequent species, Spotted Sandpiper (Fig. 20). Species frequencies in the aqua-dependent group exhibited a gradual reduction in frequency across the remaining species.

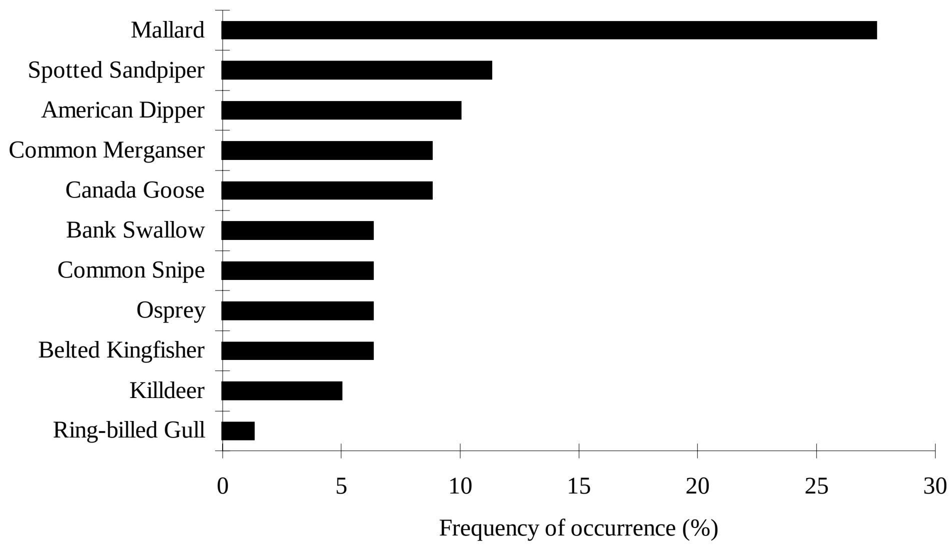

FIG. 20. Percent of sample reaches (n = 80) where each aqua-dependent bird species was observed. Data were collected in the Lake Tahoe basin, 1995 to 1996.

Riparian-associates exhibited a gradual shift in frequency of occurrence from highest to lowest frequency (Fig. 21). The 4 most frequent species were Warbling Vireo, Wilson's Warbler, Macgillivray's Warbler (*Oporonis tolmiei*), and Brown-headed Cowbird.

Upland associates exhibited a gradual shift in frequency of occurrence from highest to lowest frequency, and 14 species were present on > 80% of all reaches (Fig. 22). The frequency of occurrence of upland-associated species was generally higher compared to aquatic-dependent and riparian-meadow–associated species. Five upland associates were observed on every reach: American Robin, Mountain Chickadee, Dark-eyed Junco, Steller's Jay, and Yellow-rumped Warbler.

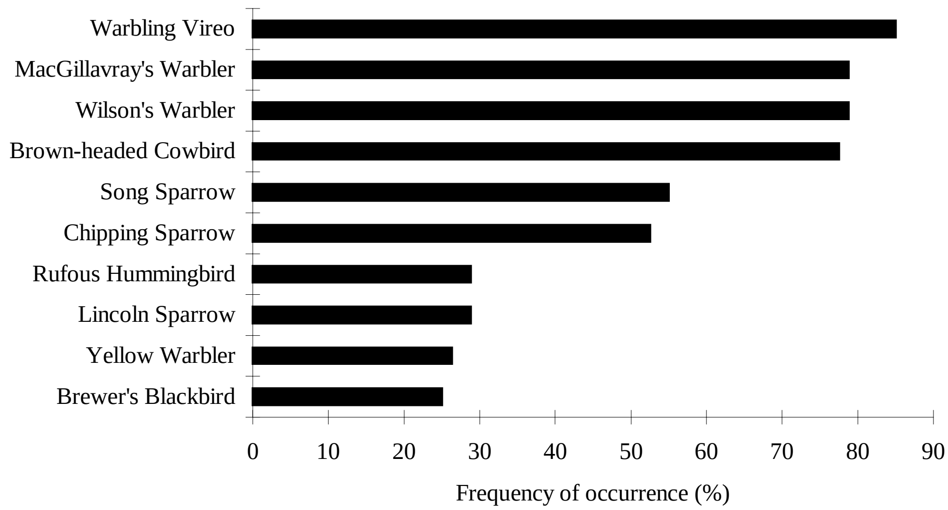

FIG. 21. Percent of sample reaches (n = 80) where each riparian-meadow–associated bird species was observed. Data were collected in the Lake Tahoe basin, 1995 to 1996.

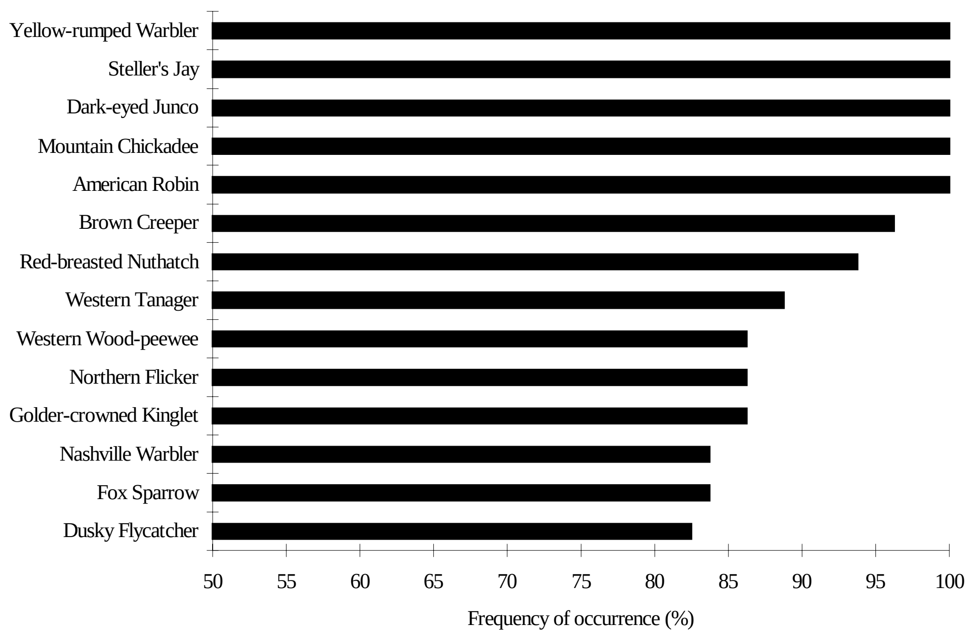

FIG. 22. Percent of sample reaches (n = 80) where each upland-associated bird species was observed. Data were collected in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of Bird Groups

Correlations

One or more of the 3 bird groups were correlated with 15 of the 22 environmental variables (Table 50). Two abiotic and 2 channel variables were correlated with bird groups. An increasingly negative correlation was observed from upland-associated to aqua-dependent. Elevation and channel gradient were increasingly negatively correlated and precipitation was decreasingly negatively correlated from upland-associated to aqua-dependent species.

Correlations with channel width shifted from positive for aqua-dependent to negative for upland-associated.

Patterns of association with vegetation types were generally similar between aqua-dependent and riparian-meadow–associated, with both differing from upland-associated species. Both aqua-dependent and riparian-meadow–associated species were negatively correlated with mixed conifer, canopy cover index, small logs, large logs, and large snags, and positively correlated with lodgepole pine, whereas these variables were not correlated with upland-associated species. Conversely, upland-associated species were positively correlated with aspen–cottonwood, whereas this variable had no correlation with the other 2 bird groups (Table 50).

TABLE 50. Significant ($P \leq 0.10$) correlations between bird species richness and 3 groups of environmental variables (n = 22) for 3 bird groups based on major habitat conditions. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive relationships, respectively. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Bird species group					
	Aqua-dependent		Riparian-meadow–associated		Upland-associated	
Environmental variable	r	*P*	r	*P*	r	*P*
Abiotic environment:						
Elevation	**-0.476**	**<0.001**	**-0.349**	**0.002**	N	n.s.
Precipitation	N	n.s.	-0.195	0.083	**-0.350**	**0.001**
Channel characteristics:						
Gradient	**-0.539**	**<0.001**	**-0.547**	**<0.001**	N	n.s.
Width	**0.365**	**0.001**	P	n.s.	**-0.418**	**<0.001**
Vegetation characteristics:						
Mixed conifer	-0.217	0.053	**-0.374**	**0.001**	P	n.s.
Lodgepole pine	**0.383**	**<0.001**	**0.378**	**0.001**	P	n.s.
Subalpine vegetation	**-0.259**	**0.021**	**-0.225**	**0.045**	**-0.245**	**0.029**
Aspen–cottonwood	P	n.s.	P	n.s.	0.212	0.059
Alder–willow	-0.217	0.053	**0.235**	**0.036**	N	n.s.
Meadow	**0.453**	**<0.001**	**0.563**	**<0.001**	**0.236**	**0.035**
Canopy cover index	**-0.379**	**0.001**	**-0.334**	**0.003**	P	n.s.
Small snags	N	n.s.	-0.202	0.073	P	n.s.
Large snags	**-0.301**	**0.007**	**-0.295**	**0.008**	P	n.s.
Small logs	**-0.279**	**0.012**	**-0.291**	**0.009**	N	n.s.
Large logs	**-0.272**	**0.015**	**-0.375**	**0.001**	N	n.s.

Regression Model for Aqua-dependent Bird Richness

The regression model for aqua-dependent bird richness in association with abiotic environmental variables consisted of a negative association with elevation (adj. R^2 = 0.220) (Table 51). The regression model with channel characteristics was a 2-variable model, with a positive association with channel width, and negative association with channel gradient (adj. R^2 = 0.313). The regression model with vegetation characteristics was a 2-variable model, with positive associations with meadow and lodgepole pine (adj. R^2 = 0.270). Backwards step-wise regression on these 5 key variables resulted in a 4-variable model where aqua-dependent bird richness increased with increases in meadow, lodgepole pine, and channel width, and decreases in elevation (adj. $R^2 = 0.451$) (Tables 51 and 52).

TABLE 51. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and the richness of 3 bird groups based on major habitat conditions. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Aqua-dependent	Riparian-meadow–associated	Upland-associated
Abiotic environment:			
Elevation	**N**	**N**	-
Precipitation	-	-	N
Channel:			
Gradient	N	**N**	N
Width	**P**	-	**N**
Vegetation:			
Lodgepole pine	**P**	P	-
Alder–willow	-	P	-
Meadow	**P**	**P**	**P**
Canopy cover index	-	-	P
Large logs	-	-	P
Variables in final model	*4*	*3*	*2*
adj. R^2	*0.515*	*0.438*	*0.197*

TABLE 52. Final regression model of key variables related to bird habitat group richness at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Environmental variable	B	SE of B	Beta	T	*P*
Aqua-dependent birds:					
Elevation	-7.387	1.481	-0.397	-4.988	<0.001
Meadow	1.906	0.394	0.396	4.833	<0.001
Channel width	0.679	0.211	0.274	3.214	0.002
Lodgepole pine	0.897	0.416	0.186	2.154	0.034
Riparian-meadow–associated birds:					
Meadow	3.715	0.857	0.416	4.337	<0.001
Gradient	-1.046	0.390	-0.275	-2.682	0.009
Elevation	-7.330	3.144	-0.212	-2.332	0.022
Upland-associated birds:					
Channel width	-3.307	0.829	-0.403	-3.988	<0.001
Meadow	3.321	1.615	0.208	2.056	0.043

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin (r = -0.515, $P < 0.001$). It is possible that the negative relationship observed between aqua-dependent bird richness (and abundance) and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible the observed relationship between aqua-dependent richness and elevation (adj. R^2 = 0.208) (Table 53).

TABLE 53. Analysis of covariance exploring the relationship between aqua-dependent bird richness and elevation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	104.05	75	1.39		
Regression	1.40	1	1.40	1.01	0.318
Elevation	30.30	3	10.10	7.28	<0.001
Model	34.34	4	8.59	6.19	<0.001
Total	138.39	79	1.75		

I looked for potential thresholds in aqua-dependent species richness in relation to the 3 variables selected in the final regression model. Only one variable, elevation, showed a threshold for aqua-dependent species richness. Aqua-dependent bird species richness dropped to $\leq$ 1 species on reaches over 2200 m in elevation (Fig. 23), and was significantly greater on reaches over 2200m in elevation (1-tailed test, pooled variance, $t = 4.40$, $P < 0.001$).

Regression Models for Riparian-meadow–associated Birds

The regression model of abiotic environmental variables consisted of a negative association with elevation (adj. R^2 = 0.111) (Table 51). The regression model of channel characteristics consisted of a negative association with channel gradient (adj. R^2 = 0.290). The regression model of vegetation variables consisted of 3 variables: positive relationships with meadow, alder–willow, and lodgepole pine (adj. R^2 = 0.436). Backwards step-wise regression on these 5 key variables resulted in a 3-variable model where the richness of riparian-meadow–associated birds increased with an increase in meadow and decreases in elevation and channel gradient (adj. R^2 = 0.438) (Tables 52 and 53).

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin (r = -0.515, $P < 0.001$). It is possible that the negative relationship observed between riparian-meadow–associated bird richness (and abundance) and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible the observed relationship between riparian-meadow–associated richness and elevation (adj. R^2 = 0.208) (Table 54).

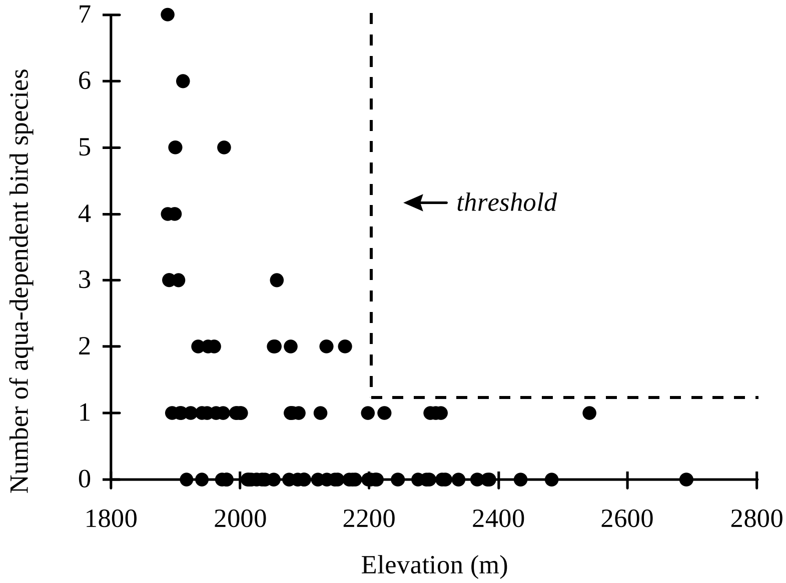

FIG. 23. Threshold between elevation and aqua-dependent bird species richness. Data were collected on 80 stream reaches in the Lake Tahoe basin, 1995 to 1996.

TABLE 54. Analysis of covariance exploring the relationship between riparian-meadow–associated bird richness and elevation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	370.14	75	4.94		
Regression	0.11	1	0.11	0.02	0.880
Elevation	54.32	3	18.11	3.67	0.016
Model	71.75	4	17.94	3.63	0.009
Total	441.89	79	5.59		

I looked for potential thresholds in riparian-meadow–associated species richness in relation to the 3 variables selected in the final regression model. Riparian-meadow–associated species richness was consistently $\geq$ 8 species where meadow comprised $\geq$ 30% of the reach area (Fig. 24), and was significantly greater where meadow exceeded 30% (1-tailed test, pooled variance, $t = 5.60$, $P < 0.001$). In relation to channel gradient, maximum species richness was approximately 50% lower on reaches with gradients $\geq$ 10% (Fig. 25). Riparian–meadow bird species richness was significantly lower on reaches with channel gradients $\geq$ 10% (1-tailed test, pooled variance, $t = 2.46$, $P = 0.009$).

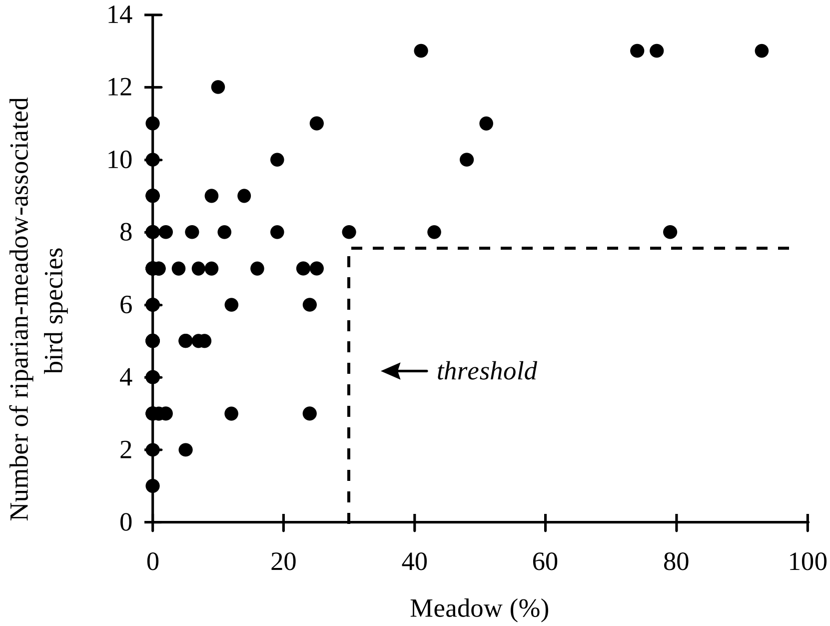

FIG. 24. Threshold between meadow and the richness of riparian-meadow–associated bird species. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

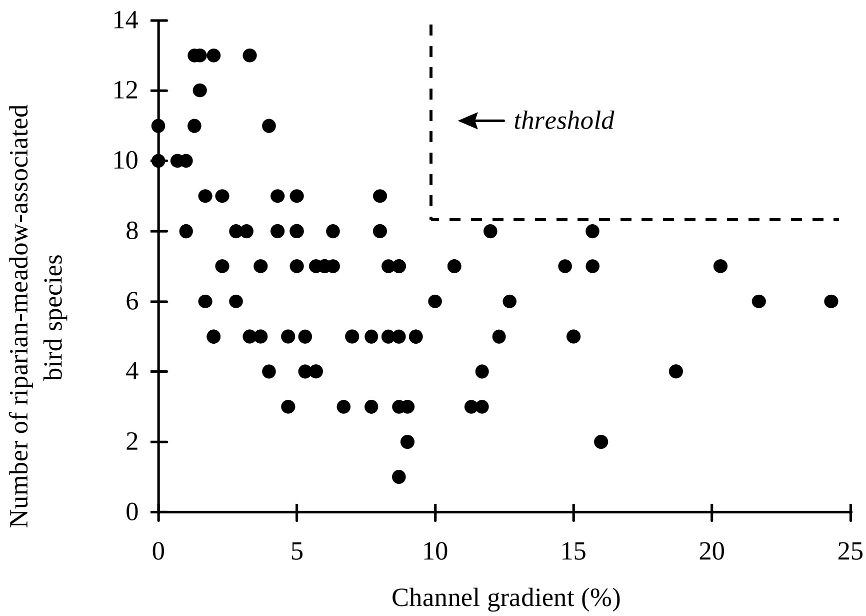

FIG. 25. Threshold between channel gradient and the richness of riparian-meadow–associated bird species. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Regression Model for Upland-associated Bird Richness

Regression on abiotic environment variables resulted in a one-variable model, a negative association with precipitation (adj. $R^2 = 0.111$) (Table 51). Regression on channel variables resulted in a 2-variable model, with negative associations with both channel width and gradient (adj. $R^2 = 0.200$). Regression on vegetation variables selected a 4-variable model: positive associations with meadow, large logs, and canopy cover index; and a negative association with subalpine conifer (adj. $R^2 = 0.139$). Backwards step-wise regression with the 7 key variables resulted in a 2-variable model, where the richness of upland-associated birds increased with increases in meadow, and decreases in channel width (adj. $R^2 = 0.197$) (Tables 52 and 53). I looked for potential thresholds in upland-associated species richness in relation to the 2 variables selected in the final regression mode, but no thresholds were observed.

Bird Group Richness by Environmental Gradients

Numerous significant correlations were observed between bird group richness and environmental gradients (Table 55). All 3 groups were negatively correlated with the elevation–precipitation gradient. Aqua-dependent and riparian-meadow–associated species were positively associated with channel flow. Aqua-dependent and riparian-meadow–associated species richness were positively correlated with the forest to meadow gradient, reiterating their association with meadow. Riparian-meadow–associated species richness was the only bird group negatively correlated with the subalpine vegetation gradient. None of the groups were correlated with the alder–willow gradient. Both the aqua-dependent and upland-associated bird groups were positively correlated with the aspen–cottonwood gradient. Few correlations existed between bird habitat groups and woody debris gradients. Aqua-dependent and riparian-meadow–associated species richness were negatively correlated with the snag and log gradient, and only the riparian–meadow associated birds showed a relationship with channel logs, being negatively correlated.

TABLE 55. Significant ($P \leq 0.10$) correlations between bird habitat group variables and principal component analysis factors. Bolded values indicate $P \leq 0.05$. r = correlation coefficients. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Bird habitat group					
	Aqua-dependent		Riparian-meadow–associated		Upland-associated	
Environmental gradient	r	*P*	r	*P*	r	*P*
Physical gradient:						
1. Elevation–precipitation	**-0.368**	**0.001**	**-0.334**	**0.002**	**-0.276**	**0.013**
2. Channel flow	**0.499**	**<0.001**	**0.367**	**0.001**	N	n.s.
Vegetation gradient:						
1. Forest to meadow	**0.470**	**<0.001**	**0.578**	**<0.001**	P	n.s.
2. Subalpine vegetation	N	n.s.	**-0.234**	**0.037**	N	n.s.
3. Alder–willow	P	n.s.	P	n.s.	N	n.s.
4. Aspen–cottonwood	**0.245**	**0.029**	P	n.s.	**0.312**	**0.005**
Woody debris gradient:						
1. Snags and logs	**-0.296**	**0.008**	**-0.370**	**0.001**	P	n.s.

Bird Group Richness by Basin Orientation

Species richness of the 3 bird groups showed different relationships with basin orientation. The richness of aqua-dependent birds varied significantly by basin orientation (ν = 3, 76; SS = 21.18, 149.81; MS = 7.06, 1,97; F = 3.58; $P = 0.018$). Richness was highest on the south side, followed by the west, then east, and was lowest on the north side of the basin. The south side had significantly greater aqua–dependent bird richness than the north based on Tukey's test. In contrast, no difference in the richness of riparian-meadow–associated birds was observed in relation to basin orientation (ANOVA, $P = 0.160$). The richness of upland associates varied significantly by basin orientation ($\nu = 3, 76$; SS = 542.56, 1339.32; MS = 180.85, 17.62; $F = 10.26$; $P < 0.001$). Richness was highest in the east, followed by the west, then north, with south having the lowest richness of upland associates. The east side had significantly greater upland bird richness than all the other orientations.

Summary of Environmental Relationships of Bird Groups

All bird groups were positively associated with meadow and negatively associated with channel gradient. Six environmental variables exhibited trends in their relationships with bird habitat groups from aqua-dependent, to riparian-meadow–associated, to upland-associated birds (Table 56). For abiotic environmental variables, I observed an increasingly positive association with elevation from aquatic to upland birds. Conversely, I observed an increasingly negative association with precipitation from aquatic to upland birds. In relation to channel characteristics, I observed an increasingly negative association with channel width from aquatic to upland birds. In relation to vegetation variables, there was a generally increasingly positive association with mixed conifer and increasingly negative association with lodgepole pine from aquatic to upland birds. In addition, aqua-dependent and riparian-meadow–associated bird groups had a more negative association with canopy cover index. This is consistent with their positive association with meadow and lodgepole pine habitats, which have lesser amounts of woody material (living or dead) compared to other vegetation types.

TABLE 56. Summary of regression relationships between bird habitat groups and environmental variables that showed a gradient of change from aqua-dependent to upland-associated. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Bird habitat group: Aqua-dependent	Riparian-meadow–associated	Upland-associated
Abiotic environment:	———	Elevation	——→
	←——	Precipitation	———
Channel:	←——	Width	———
Vegetation:	———	Canopy cover index	——→
	———	Large logs	——→
	←——	Lodgepole pine	———

The 6 environmental variables that showed a pattern of association across bird species groups were graphed against each group to identify potential environmental thresholds. All but 4 of the 18 relationships showed either no patterned relationship or a steadily increasing or decreasing pattern. Two environmental thresholds were indicated for aqua-dependent bird species, with elevation (described previously) and canopy cover index. Although canopy cover index was not selected for the regression model, aqua-dependent bird species richness exhibited a potential threshold with this variable, where the highest number of aqua-dependent species were only observed where canopy cover index was < 20% (Fig. 26). Aqua-dependent bird richness was significantly greater where canopy cover index was < 20% (1-tailed test, pooled variance, $t = 3.37$, $P = 0.002$). Two environmental thresholds were indicated for riparian-meadow–associated bird species, with meadow (described previously) and lodgepole pine. Although lodgepole pine was not selected for the regression model, riparian-meadow–associated species richness exhibited a potential threshold with this variable, being consistently ≥ 6 species where there was any amount of lodgepole pine vegetation (Fig. 27). Riparian–meadow bird species richness was significantly greater on reaches where lodgepole pine was present (1-tailed test, pooled variance, $t = 3.57$, $P < 0.001$).

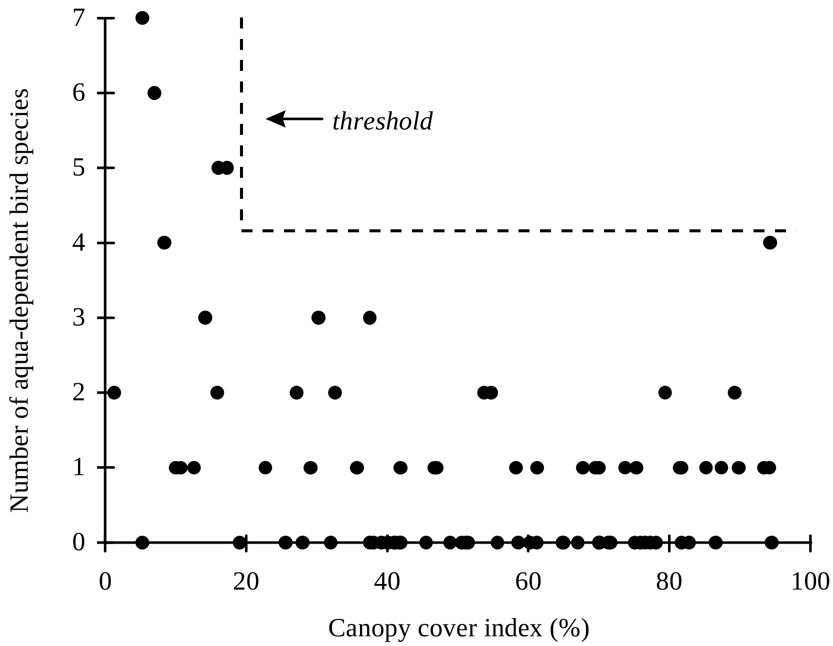

FIG. 26. Threshold between canopy cover index (as measured by a spherical convex densiometer) and the richness of aqua-dependent bird species. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

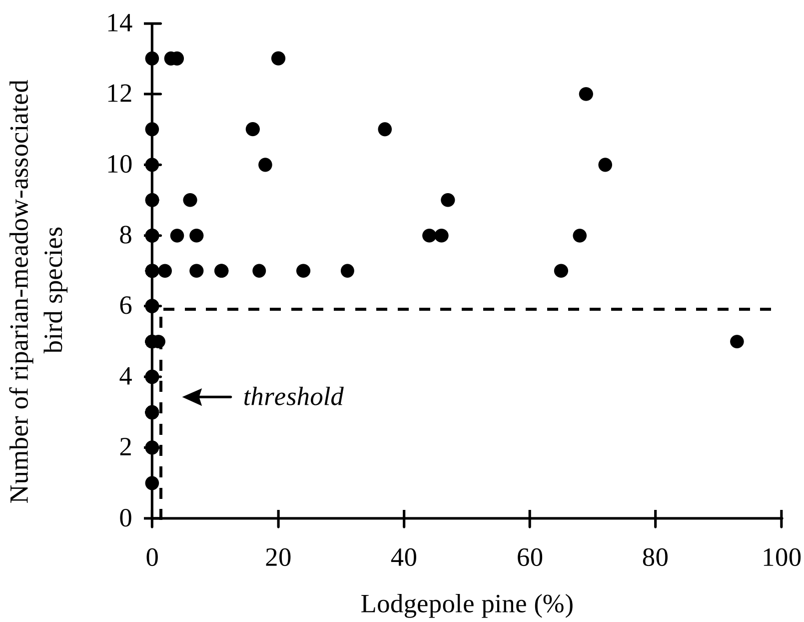

FIG. 27. Threshold between lodgepole pine and the richness of riparian-meadow–associated bird species. Data were collected on 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Patterns of Rarity

General Patterns

The distribution of relative frequencies of species showed that over 50% of the species (54 of 101) were present on less than 25% of the reaches (Fig. 28). Forty species were present on < 10% of the reaches. Each rare species occurred on an average of 3.1 reaches (SE = 0.30) (Table 57), and at least one rare species was present on 87.7% of the reaches. Each common species occurred on an average of 34.1 reaches (SE = 0.62), and at least 20 of the common species were observed on every reach (Table 51). The correlation between the number of rare and common species per reach was moderately strong and significant (r = 0.281, $P = 0.012$).

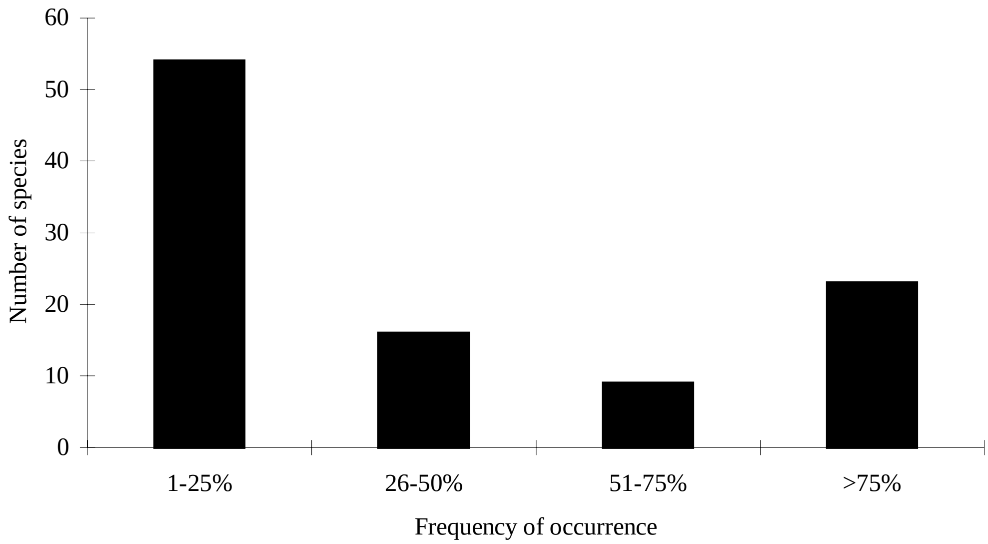

FIG. 28. Frequency of occurrence of bird species. Data were collected on 80 stream reaches in the Lake Tahoe basin, 1995 to 1996.

TABLE 57. Descriptive statistics for measures of frequency for bird occurrence. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Frequency variable	Minimum	Maximum	Average	SE
Number of rare species	0	13	3.1	0.30
Number of common species	20	44	34.1	0.62
Percent rare species	0	28.3	7.8	0.65
Percent common species	71.7	100.0	92.2	0.65

I also calculated the proportion of the bird assemblage comprising each frequency class. The proportion of rare species averaged 7.8 %, whereas the proportion of common species averaged 92.2 % per reach (Table 57).

Significant correlations were observed among the 4 measures of rarity (Table 58). The high correlations between number of rare species and the percent of both rare and common species indicated that the most informative patterns of association could be discerned by analyzing the absolute number of rare and common species.

TABLE 58. Significant ($P \leq 0.10$) correlations among bird frequency variables. Bolded values indicate $P \leq 0.05$. Shading indicates redundant cells. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Number of rare species		Number of common species		Percent rare species	
Frequency variables	r	*P*	r	*P*	r	*P*
Number of rare species						
Number of common species	0.281	0.012				
Percent rare species	**0.981**	**<0.001**	0.170	0.133		
Percent common species	**-0.981**	**<0.001**	-0.170	0.133	**-1.000**	**<0.001**

Environmental Relationships of Bird Rarity

Correlations

Correlations showed relationships with many physical and vegetation characteristics (Table 59). A shift from negative to neutral correlation with elevation and channel gradient was observed between the richness of rare and the richness of common species. In addition, shifts from neutral to positive correlation with channel width and from positive to neutral correlation with sinuosity was observed between the richness of rare and the richness of common species. These patterns indicate that rare species were more diverse at lower elevation reaches with wide channels, low gradients, and higher sinuosity, suggesting rare species are more closely associated with aquatic environments.

Vegetation characteristics also showed patterned relationships with bird frequency classes. Six vegetation variables showed shifts from negative association with rare species to neutral association with common species: aspen–cottonwood, mixed conifer, canopy cover index, large snags, small snags, large logs, and small logs. One variable, subalpine conifer, had increasingly negative association from rare to common species. Rare and common species were both more diverse where there was a greater proportion of meadow and less diverse where there was a greater proportion of subalpine conifer.

Regression Model for Rare Bird Species

Regression models for each frequency class reflected the bivariate relationships observed (Table 60). The number of rare species was associated with 2 abiotic environmental variables (negative relationship with elevation and south aspects, adj. $R^2 = 0.134$), with one channel variable (negative relationship with gradient, adj. $R^2 = 0.266$), and with one vegetation variable (positive relationship with meadow, adj. $R^2 = 0.391$). A final backwards stepwise regression on these 4 key variables resulted in a 3-variable model where the richness of rare bird species increased with increases in meadow and decreases in elevation and channel gradient (adj. $R^2 = 0.489$) (Tables 60 and 61).

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ($r = -0.515$, $P < 0.001$). It is possible that the negative relationship observed between the number of rare birds and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible for the observed relationship between rare bird richness and elevation (adj. $R^2 = 0.188$) (Table 62).

TABLE 59. Significant ($P \leq 0.10$) correlations between bird frequency class variables and normalized environmental variables at reaches (n = 80) in the Lake Tahoe basin sampled 1995 to 1996. Bolded values indicate $P \leq 0.05$.

	Number of bird species in each frequency class			
	Rare species		Common species	
Environmental variable	r	*P*	r	*P*
Abiotic environment:				
Elevation	**-0.342**	**0.002**	N	n.s.
Precipitation	**-0.238**	**0.034**	**-0.267**	**0.017**
Channel characteristics:				
Gradient	**-0.525**	**<0.001**	N	n.s.
Width	P	n.s.	**0.348**	**0.002**
Sinuosity	**0.281**	**0.011**	P	n.s.
Vegetation characteristics:				
Mixed conifer	**-0.292**	**0.009**	N	n.s.
Lodgepole pine	**0.280**	**0.012**	P	n.s.
Subalpine conifer	-0.198	0.078	-0.208	0.064
Aspen–cottonwood	P	n.s.	**0.249**	**0.026**
Meadow	**0.631**	**<0.001**	**0.266**	**0.017**
Canopy cover index	**-0.366**	**0.001**	P	n.s.
Small snags	**-0.265**	**0.018**	P	n.s.
Large snags	**-0.335**	**0.002**	P	n.s.
Small logs	**-0.387**	**<0.001**	N	n.s.
Large logs	**-0.373**	**0.001**	N	n.s.

TABLE 60. Variables selected in step-wise regressions between 3 groups environmental variables (n = 22) and the number of species in each of 2 frequency classes. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Rare species	Common species
Abiotic environment:		
Elevation	**N**	-
Precipitation	-	N
South aspect	N	-
Channel characteristics:		
Width	-	**N**
Gradient	**N**	N
Vegetation characteristics:		
Aspen–cottonwood	-	P
Alder–willow	-	P
Meadow	**P**	**P**
Large snags	-	P
Variables in final model	*3*	*2*
adj. R^2	*0.489*	*0.159*

TABLE 61. Final regression model of key environmental variables related to bird frequency classes at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Number of rare species:					
Meadow	4.525	0.799	0.518	5.660	<0.001
Elevation	-7.534	2.934	-0.223	-2.568	0.012
Gradient	-0.750	0.364	-0.201	-2.059	0.043
Number of common species:					
Channel width	-3.068	0.959	-0.331	-3.200	0.002
Meadow	4.393	1.868	0.243	2.352	0.021

TABLE 62. Analysis of covariance exploring the relationship between the number of rare bird species and elevation with disturbance as a covariate. SS = sum of squares. ν = degrees of freedom. MS = mean square.

Source of variation	ν	SS	MS	F	*P*
Within + residual	75	434.42	5.79		
Regression	1	3.48	3.48	0.60	0.441
Elevation	3	112.38	37.46	6.47	0.001
Model	4	128.78	32.20	5.56	0.001
Total	79	563.20	7.13		

Regression Model for Common Bird Species

The common bird species group exhibited different relationships with environmental relationships compared to the rare species group (Table 60). The number of common bird species was associated with one abiotic environmental variable (negative relationship with precipitation, adj. $R^2 = 0.059$), 2 channel characteristics (negative relationships with gradient and width, adj. $R^2 = 0.178$), and 4 vegetation characteristics (positive relationships with meadow, alder willow, aspen cottonwood, and large logs, adj. $R^2 = 0.148$). A final backwards stepwise regression on these 7 key variables resulted in a 2-variable model where the richness of common bird species increased with increases in meadow and decreases in channel width (adj. $R^2 = 0.159$) (Tables 61 and 62).

Bird Rarity by Environmental Gradients

Frequency classes were compared to physical gradients to explore patterns of association (Table 63). The numbers of species in both frequency classes were negatively correlated with physical factor 1 (elevation–precipitation). Rare species richness was positively correlated with physical factor 2 (channel flow), and common species richness was not correlated with any physical factors. This indicates that the richness of all species was higher at lower elevation and precipitation, but that a greater number of rare species occurred in association with slow, wide streams.

TABLE 63. Significant ($P \leq 0.10$) correlations between bird frequency class variables and principal component analysis factors. Bolded values indicate $P \leq 0.05$. r = correlation coefficients. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Number of bird species in frequency classes			
	Rare species		Common species	
Environmental gradient	r	*P*	r	*P*
Physical gradient:				
1. Elevation–precipitation	**-0.370**	**0.001**	**-0.200**	**0.076**
2. Channel flow	**0.374**	**0.001**	N	n.s.
Vegetation gradient:				
1. Forest to meadow	**0.567**	**<0.001**	**0.227**	**0.043**
2. Subalpine vegetation	N	n.s.	N	n.s.
3. Alder–willow	N	n.s.	P	n.s.
4. Aspen–cottonwood	P	n.s.	**0.309**	**0.005**
Woody debris gradient:				
1. Snag and log	**-0.434**	**<0.001**	P	n.s.

Frequency classes were compared to the vegetation and woody debris PCA scores to explore patterns of association (Table 63). The number of species in both frequency classes was positively correlated with the forest to meadow gradient. Common species richness was also positively correlated with the aspen–cottonwood gradient. Rare species richness was negatively correlated with the snag and log gradient (Table 63).

Bird Rarity by Basin Orientation

The number of species in each bird frequency class was significantly different among basin orientations. The number of rare species was greater on the south and east sides of the basin compared to the north side (ANOVA, $\nu = 3, 76$; SS = 80.00, 483.20; MS = 26.67, 6.36; F = 4.19; $P = 0.008$). The number of common species was greater the east side of the basin compared to all other orientations (ANOVA, $\nu = 3, 76$; SS = 550.22, 1852.17; MS = 183.41, 24.37; F = 7.53; $P < 0.001$) .

Patterns of Bird Beta Diversity

Bird Species Turnover Along Environmental Gradients

Species Turnover

The lower of the gains and losses between any two segments represented the beta diversity for the 2 segments - the change in composition that was independent from alpha diversity. The sum of beta diversity across all 3 segment comparisons, "total turnover", was used as the primary indication of the contribution of a gradient to beta diversity (Table 64). The channel flow gradient had the highest species turnover ($n = 23$), followed by 3 gradients with the same species turnover ($n = 21$): subalpine vegetation, snags and logs, and aspen–cottonwood. All 6 of the remaining gradients ranged in species turnover from 18 to 20.

Patterns of turnover along each gradient provide additional insights as to their contributions to beta diversity (Table 64). For the elevation gradient, total richness declined from low to high segments, and turnover was greatest mid gradient. Total richness declined from low to high segments along the precipitation gradient, as did turnover. The elevation–precipitation gradient was a mixed reflection of elevation and precipitation. Total richness increased and turnover decreased with channel flow gradient. Along the forest to meadow gradient, total richness increased, but turnover generally decreased. Richness and turnover varied along the subalpine vegetation and alder–willow gradients. Aspen–cottonwood was associated with increased richness and minor variation in turnover. Finally, total richness declined along the snag and log gradient, but turnover was generally higher at the upper end of the gradient.

Whittaker's Index of Beta Diversity

The gradients were evaluated for their relative contribution to beta diversity in part based on a modified Whittaker's beta diversity index (β_{wMIN}), with the unmodified index value provided for comparison (Table 64). The average β_{wMIN} for segment comparisons along each gradient varied from a low of 0.072 for forest to meadow and elevation–precipitation, to a high of 0.093 for the channel flow gradient. Next to channel flow, the snag and log, aspen–cottonwood, elevation, and subalpine vegetation gradients had the next highest β_{wMIN} values (0.085, 0.083, 0.082, and 0.080, respectively). The remaining gradients had much lower β_{wMIN} values.

TABLE 64. Beta diversity index values for birds within and among 9 environmental gradients. The number of species per segment, the number of species only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. Bolded values indicate species turnover related to beta diversity. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	β_w*	β_{wMIN}†
Elevation:							
seg1:seg2	89	77	95	**6**	18	0.145	0.067
seg2:seg3	77	78	87	10	**9**	0.123	0.115
seg3:seg4	78	73	83	**5**	10	0.099	0.064
average							*0.082*
low:high	*95*	*83*	*101*	***6***	*18*	*0.135*	*0.063*
Precipitation:							
seg1:seg2	87	88	97	10	**9**	0.109	0.102
seg2:seg3	88	80	94	**6**	14	0.119	0.068
seg3:seg4	80	76	84	**4**	8	0.077	0.050
average							*0.073*
low:high	*97*	*84*	*101*	***4***	*17*	*0.116*	*0.041*
Elevation–precipitation:							
seg1:seg2	89	84	98	**9**	14	0.133	0.101
seg2:seg3	84	76	87	**3**	11	0.088	0.036
seg3:seg4	76	70	82	**6**	12	0.123	0.079
average							*0.072*
low:high	*98*	*82*	*101*	***3***	*19*	*0.122*	*0.031*
Channel flow:							
seg1:seg2	77	77	87	10	**10**	0.130	0.130
seg2:seg3	77	86	93	16	**7**	0.141	0.081
seg3:seg4	86	88	94	8	**6**	0.080	0.068
average							*0.093*
low:high	*87*	*94*	*101*	*14*	***7***	*0.116*	*0.074*
Forest to meadow:							
seg1:seg2	72	82	88	16	**6**	0.143	0.073
seg2:seg3	82	75	91	**9**	16	0.159	0.110
seg3:seg4	75	93	96	21	**3**	0.143	0.032
average							*0.072*
low:high	*88*	*96*	*101*	*13*	***5***	*0.098*	*0.052*

TABLE 64 cont.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	β_w*	β_{wMIN}†
Subalpine vegetation:							
seg1:seg2	76	87	91	15	**4**	0.117	0.046
seg2:seg3	87	88	98	11	**10**	0.120	0.114
seg3:seg4	88	84	95	**7**	11	0.105	0.080
average							*0.080*
low:high	*91*	*95*	*101*	*10*	***6***	*0.086*	*0.063*
Alder–willow:							
seg1:seg2	92	84	96	**4**	12	0.091	0.043
seg2:seg3	84	77	93	**9**	16	0.155	0.107
seg3:seg4	77	81	87	10	**6**	0.101	0.074
average							*0.075*
low:high	*96*	*87*	*101*	***5***	*14*	*0.104*	*0.052*
Aspen–cottonwood:							
seg1:seg2	77	73	83	**6**	10	0.107	0.078
seg2:seg3	73	85	93	20	**8**	0.177	0.094
seg3:seg4	85	91	98	13	**7**	0.114	0.077
average							*0.083*
low:high	*83*	*98*	*101*	*18*	***3***	*0.116*	*0.031*
Snag and log:							
seg1:seg2	91	74	95	**4**	21	0.152	0.044
seg2:seg3	74	81	90	16	**9**	0.161	0.111
seg3:seg4	81	81	89	8	**8**	0.099	0.099
average							*0.084*
low:high	*95*	*89*	*101*	***6***	*12*	*0.098*	*0.063*

* Whittaker's beta diversity index: S/α - 1, where S = total species richness, and α = the average species richness of the two segments being compared.

† Modified Whittaker's beta diversity index: (S/s-max) - 1, where S = total species richness, and s-max = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

Species Presence

Species presence contributions to beta diversity are displayed in Table 65. Species contributing to gains and losses between lower and upper segments of each gradient are indicated, along with species showing additional trends of presence (absent from segment 1 or 4) along the gradient. Species specific associations with gradients also indicate the relevance of the gradient to individual species. Most species had frequencies < 10%. Elevation and precipitation were analyzed separately, as well as their combined representation in the elevation–precipitation gradient. Along the elevation gradient, only 2 of the 6 species associated only with the upper elevations were present on greater than one reach. Lazuli Bunting (*Passerina amoena*) and Common Raven only occurred at higher elevation reaches. An additional 3 species were absent from the lowest elevation reaches: Blue Grouse (*Dendragapus obscurus*), American Dipper

(*Cinclus mexicanus*), and Ruby-crowned Kinglet (*Regulus calendula*). A much larger number of species were associated with lower elevation reaches, reflecting the negative relationship between alpha diversity and elevation. Eleven of the 18 species associated with lower elevations occurred on 2 or more reaches. Six of these 11 species occurred in only segment 1, including Canada Goose, Ring-billed Gull, Western Meadowlark (*Sturnella neglecta*), Barn Swallow (*Hirundo rustica*), American Crow (*Corvus brachyrhynchos*), and Bank Swallow (*Riparia riparia*), the most elevationally restricted species. An additional 6 species were absent from the highest elevation reaches, including 3 species with frequencies $\geq$ 10%: Spotted Sandpiper, Tree Swallow (*Tachycineta bicolor)*, and Spotted Towhee (*Pipilo erythrophthalmus*). Precipitation had fewer species absent from one end of the gradient compared to the elevation gradient. Only 2 of the 4 species associated with only the upper portion of the gradient occurred on more than 1 reach; Swainson's Thrush (*Catharus ustulatus*) occurred only in segment 4, and Winter Wren (*Troglodytes troglodytes*) occurred only in segments 3 and 4. These species are mesic habitat associates. An additional 4 species were absent from the driest reaches, including Common Snipe (*Gallinago sericea*), Pine Grosbeak, (*Pinicola enucleator*) Cooper's Hawk (*Accipiter cooperi*), and Bushtit (*Psaltriparus minimus*). Pine Grosbeak is notable in that it also has a frequency of $\geq$ 10%. A greater number of species were associated with the drier end of the precipitation gradient, reflecting the negative relationship between alpha diversity and precipitation. Seven of the 17 species absent from the upper end of the precipitation gradient occurred on more than 1 reach. An additional 5 species were absent from the highest precipitation reaches.

The combined elevation–precipitation gradient reflected part of both the elevation and precipitation gradients, and generally showed a weaker relationship with species turnover than either of the individual gradients. Along the combined elevation–precipitation gradient, the fewest species (n = 3) were associated with the upper end of the elevation–precipitation gradient. The Common Raven (*Corvus corax*) and American Dipper were absent from segment 1 of the elevation–precipitation gradient, and Winter Wren was absent from both segment 1 and 2. Thirteen of the 18 species only present with the lower end of the gradient were present on more than one reach. This large number of species absent from segments 3 and 4 (n = 7) and segment 4 only (n = 6), reflect the negative relationship between elevation–precipitation and alpha diversity. Osprey (*Pandion haliaetus*), American Crow, Black-headed Grosbeak (*Pheucticus melanocephalus*), Black-billed Magpie (*Pica pica*), and 4 swallow species were restricted to lower elevation reaches. Black-headed Grosbeak was notable in that it had a frequency $\geq$ 10%.

Along the channel flow gradient, the fewest species were associated with the lower end of the other abiotic gradient. Common Raven, Northern Pygmy Owl (*Glaucidium gnoma*), and Mountain Bluebird (*Sialia currocoides*) comprise the subset of the 7 species absent from the upper end of the gradient that occurred on more than one reach. Additionally, Turkey Vulture (*Cathartes aura*) and Blue Grouse were absent from segment 4. Seven of the 14 species only present within the upper end of the gradient were present on more than one reach. This large number of species absent from segments 1 and 2 (n = 7) and segment 1 (n = 6), reflect the negative relationship between channel flow and alpha diversity. Spotted Sandpiper was notable in that it was absent from segment 1 and had a frequency $\geq$ 10%.

TABLE 65. Species present on 2 or more reaches and absent from lower or upper segments of each of 2 abiotic environmental gradient. Gradients were defined by principal components analysis. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Elevation gradient low < ----------------- > high				Precipitation gradient low < ----------------- > high				Elevation–precipitation gradient low < ----------------- > high				Channel flow gradient low < ------------------ > high			
Species	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:																
Barn Swallow	X_1				X				X_1							X
American Crow	X_1				X				X_1							X
Western Meadowlark	X_1				X											X
Ring-billed Gull	X_1				X											X
Bank Swallow	X_1					X			X_1						X	
Cliff Swallow	X					X			X							X
Canada Goose	X_1									X						
Belted Kingfisher	X									X						X
Pacific-slope Flycatcher	X									X						
Black-throated Gray Warbler	X									X						
Swainson's Thrush	X							X								X
Killdeer		X							X							
Black-billed Magpie		X			X				X							
Osprey		X				X			X						X	
Blue Grouse			X			X								X		
Ruby-crowned Kinglet			X													
Common Raven				X		X					X		X			
Lasuli Bunting				X												
Turkey Vulture					X					X				X		
Lesser Goldfinch					X											
Bushtit							X								X	
Common Snipe							X								X	
Cooper's Hawk							X									
Pine Grosbeak							X									

TABLE 65 cont.

Species	Elevation gradient low < ----------------- > high				Precipitation gradient low < ----------------- > high				Elevation–precipitation gradient low < ----------------- > high				Channel flow gradient low < ------------------ > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10% cont.:																
Winter Wren								X				X				
Tree Swallow										X					X	
Northern Pygmy Owl													X			
Mountain Bluebird													X			
Frequency ≥ 10%:																
Spotted Sandpiper		X													X	
Tree Swallow		X														
Spotted Towhee		X														
American Dipper			X								X					
Black-headed Grosbeak										X						
Summary	11	6	3	2	7	5	4	2	7	6	2	1	3	2	6	7

[1] Only occurs on segment 1.

A number of species were associated with each end of the snag and log gradient (Table 66). Fewer species (n = 4) were absent at the lower end of the snag and log gradient compared to the upper end (n = 18). Swainson's Thrush was absent from both segment 1 and 2, and Black-throated Gray Warbler, Winter Wren, and Ruby-crowned Kinglet were absent from segment 1 of the snag and log gradient. These species were not present at low densities of snags and logs. Eight of the 12 species present only at the lower end of the gradient (Table 64) were present on more than one reach (Table 66). The large number of species absent from segment 4 or segments 3 and 4 reflect the negative relationship between snag and log densities and alpha diversity. These species consisted of open-habitat associates, such as Western Meadowlark, White-crowned Sparrow (*Zonotrichia leucophrys*), Mountain Bluebird, and Lesser Goldfinch (*Carduelis psaltria*), and aquatic habitat associates such as Osprey, Barn Swallow, and Ring-billed Gull. White-crowned Sparrow was notable in that it was the only species absent from high snag and log densities that had a frequency of $\geq$ 10%.

TABLE 66. Species present on 2 or more reaches and absent from lower or upper segments of the snag and log gradient (derived by principal components analysis). Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Snag and log gradient low < ----------------------- > high			
Species	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:				
Western Meadowlark	X_1			
Ring-billed Gull	X_1			
Barn Swallow	X			
Osprey	X			
Common Raven	X			
Lesser Goldfinch	X			
Mountain Bluebird		X		
Black-throated Gray Warbler			X	
Winter Wren			X	
Ruby-crowned Kinglet			X	
Swainson's Thrush				X_4
Frequency $\geq$ 10%:				
White-crowned Sparrow	X			
Summary	7	1	3	1

$_1$ Only occurs on segment 1.
$_4$ Only occurs on segment 4.

A moderate number of species were absent from either end of each of the 4 vegetation gradients (Table 67). Almost all of the species absent from either end of the forest to meadow gradient were associated with the meadow end of the gradient, reflecting the positive relationship between alpha diversity and the forest to meadow gradient. Only one of the 5 species only associated with the forest end of the gradient was present on more than one reach, Black-throated

Gray Warbler. This species was only present in mixed conifer forests. Five of the 13 species gained from low to high ends of the gradient were present on more than reach, consisting of 3 open-habitat associated species only observed on segment 4 (Western Meadowlark, Ring-billed Gull, and Barn Swallow) and the 2 additional species only observed on segments 3 and 4 (American Crow and Belted Kingfisher [*Ceryle alcyon*]). Five additional species were absent from segment 1 only. These species represent the contribution of this gradient to beta diversity. Along the subalpine vegetation gradient, only one of the 6 species lost from low to high ends of the gradient was present on more than one reach, the Bushtit. An additional 3 species were absent from the upper most segment of the gradient, including Pacific-slope Flycatcher (*Empidonax difficilis*), and 2 species with frequencies $\geq$ 10%, the Spotted Sandpiper and Mallard. All of these 3 species were absent from high elevation vegetation types. Four of the 10 species absent from the lower end of the gradient were present on 2 or more reaches, including Common Raven, Lesser Goldfinch, Swainson's Thrush, and Northern Pygmy Owl. All of these species were only present in vegetation characteristic of higher elevations. An additional 6 species were absent from segment 1 only. Along the alder–willow gradient, more species were lost than gained as alder–willow become more dominant. Five of the 14 species only associated with the low end of the gradient occurred on more than one reach, and consisted of primarily open-habitat associated species such as Barn Swallow, Western Meadowlark, Ring-billed Gull, and Lesser Goldfinch. The one exception was Northern Goshawk (*Accipiter gentilis*), which was also absent from reaches with large proportions occupied by alder–willow. Two Corvid species, American Crow and Black-billed Magpie, were absent from the highest segment of the alder–willow gradient. Alternatively, 3 of the 5 species only found in the upper segments of the alder–willow gradient were present on 2 or more reaches, and included shrub associates Bushtit and Swainson's Thrush, as well as the Common Snipe. Finally, the aspen–cottonwood gradient had far more species gained than lost from the lower to upper ends of the gradient, reflecting its positive association with alpha diversity. One of the 3 species associated with only the lower end of the aspen–cottonwood gradient occurred on more than one reach, Cooper's Hawk. At the other end of the gradient, 9 of the 18 species only found in segments 3 and 4 occurred on more than one reach. Aspen and cottonwood stands are often associated with meadows, and so many of the species were open-habitat associates such has Western Meadowlark, Barn Swallow, Osprey, Killdeer, and Lesser Goldfinch. However, the Northern Pygmy Owl is a forest associate and appeared to find aspen–cottonwood stands favorable habitat. Four additional species were absent from segment 1, including the Spotted Towhee, a species with $\geq$ 10% frequency.

Ranking Gradients for Beta Diversity

The 8 environmental gradients were ranked to reflect their contribution to beta diversity based on species turnover and the modified Whittaker's index (Table 68). Channel flow was ranked the highest contributor to species turnover, with 23 species turning over along the length of the gradient, 18 of which were present on 2 or more reaches. It also had the highest average Whittaker's beta diversity index. Aspen–cottonwood was the second highest ranking gradient, followed by snags and logs, subalpine vegetation and elevation. The combined elevation–precipitation gradient was not ranked in Table 68 because it was redundant with the individual elevation and precipitation gradients, however as a point of comparison it would have ranked between alder–willow (8th) and forest to meadow (9th) (species turnover = 18, species turning over with frequency $\geq 2 = 16$, $\beta_{wMIN} = 0.072$). Apparently the combined elevation–precipitation gradient muddled somewhat the individual contributions of each gradient to beta diversity.

TABLE 67. Species present on 2 or more reaches and absent from lower or upper segments of each of 4 vegetation gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Forest to meadow gradient low < ----------------- > high				Subalpine veg. gradient low < ----------------- > high				Alder–willow gradient low < ---------------- > high				Aspen–cottonwood gradient low < ----------------- > high			
Species	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency < 10%:																
Black-throated Gray Warbler	X															
Common Snipe			X									X				
Blue Grouse			X													
Common Raven			X					X								
Killdeer			X													X
Pacific-slope Flycatcher			X			X										
Western Meadowlark				X_4					X							X
Ring-billed Gull				X_4					X_1							X
Barn Swallow				X_4			X		X							X
American Crow				X			X			X						X
Belted Kingfisher				X												
Cliff Swallow							X									
Bank Swallow							X									X
Osprey							X									X
Winter Wren							X									
Lesser Goldfinch								X	X							X_4
Swainson's Thrush								X				X_4				
Northern Pygmy Owl								X								X
Northern Goshawk									X							
Black-billed Magpie										X					X	
Bushtit					X							X			X	
Cooper's Hawk													X			
Ruby-crowned Kinglet															X	

TABLE 67 cont.

Species	Forest to meadow gradient low < -----------------> high				Subalpine veg. gradient low < -----------------> high				Alder–willow gradient low < ----------------> high				Aspen–cottonwood gradient low < -----------------> high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Frequency ≥ 10%:																
Spotted Sandpiper						X										
Mallard						X										
Spotted Towhee															X	
Summary	1	0	5	5	1	3	6	4	5	2	0	3	1	0	4	9

[1] Only occurs on segment 1.

[4] Only occurs on segment 4.

TABLE 68. Ranking of environmental gradients by their contribution to bird beta diversity in the Lake Tahoe basin.

Environmental gradient	Total turnover	Core turnover - freq. ≥ 2 reaches	Average β_{wMIN}	Rank
Channel flow	23	18	0.093	1
Aspen–cottonwood	21	14	0.083	2
Snag and log	21	12	0.085	3
Subalpine vegetation	21	9	0.080	4
Elevation	20	22	0.082	5
Precipitation	19	18	0.073	6
Alder–willow	19	11	0.075	7
Forest to meadow	18	12	0.072	8

Bird Species Turnover by Basin Orientation

Basin orientation can affect species turnover, as did the environmental gradients discussed above. All pair-wise comparisons of orientations were conducted to assess the contribution of basin orientation to species turnover (Table 69). Based on the average β_{wMIN} across all orientation comparisons, orientation has a relatively high contribution to beta diversity compared to the environmental gradients analyzed. Only channel flow had a higher β_{wMIN} index value. However, the lowest number of turnovers was 4, occurring between north and east orientations. The remaining number of turnovers was 6 (n = 2), 7 (n = 1), 9 (n = 1), and 11 (n = 1). The number of turnovers between the east and south orientations (n = 11) and between north and south orientations (n = 9) exceeded the highest number of turnovers observed between the lower and upper portions of the environmental gradients. It was not possible to compare patterns of species turnover between basin orientation and the other gradients because orientations can not be aligned along a linear gradient, however the comparison of east–dry and west–wet orientations provides a representation of all orientation comparisons, and the species turnover between these sides of the basin was high (n = 8).

Species absent from one or more orientations provide species specific contributions to the gains and losses observed between orientations (Table 70). Approximately twice as many species were absent from the north side of the basin compared to any of the other three orientations. The east, south, and west sides of the basin had a similar number of species absent. Only 2 species were present in only one orientation; Ring-billed gull was present only on the south side and Swainson's Thrush was present only on the west side of the basin. Only the Winter Wren was restricted to the 2 wetter orientations (south and west). Three species were restricted to the 2 drier orientations (north and east): Common Raven, Northern Pygmy Owl, and Turkey Vulture. The 9 species absent from the east orientation may be limited by xeric conditions or otherwise limited to the Great Basin zoogeographic region, with the greatest possibility existing for species with frequency $\geq$ 10%, including Pine Grosbeak, Spotted Sandpiper, and Rufous Hummingbird (*Selasphorus rufus*). Similarly, the 10 species absent from the west orientation may be limited by mesic conditions or otherwise limited to the Sierra Nevada zoogeographic region, with the greatest possibility existing for species with frequency $\geq$ 10%, including Common Nighthawk (*Chordeiles minor*) and White-crowned Sparrow.

TABLE 69. Beta diversity index values for birds among basin orientations. The number of species per segment, the number of species only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. N = north, E = east, S = south, W = west side of the basin. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Basin orientation comparison	Richness of first segment	Richness of second segment	Total richness	Gains	Losses	β_w*	β_{wMIN}†
N:E	73	86	92	19	**4**	0.157	0.070
E:S	86	86	97	**11**	12	0.128	0.128
S:W	86	81	93	**7**	12	0.114	0.081
N:S	73	86	92	**9**	14	0.157	0.070
E:W	86	81	95	19	**6**	0.138	0.105
N:W	73	81	87	14	**6**	0.130	0.074
average							*0.088*
N and E:S and W	*92*	*93*	*101*	*9*	***8***	*0.092*	*0.086*

* Whittaker's beta diversity index: S/α - 1, where S = total species richness, and α = the average species richness of the two segments being compared.

† Modified Whittaker's beta diversity index: (S/s-max) - 1, where S = total species richness, and s-max = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

TABLE 70. Bird species present on greater than one reach and absent from one or more basin orientations. X's indicate where species was present. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

	Basin orientation			
Bird species	North side (*n* = 20)	East side (*n* = 20)	South side (*n* = 16)	West side (*n* = 24)
Frequency < 10%:				
Cooper's Hawk	X		X	X
Common Snipe	X		X	X
Bushtit	X			X
Lasuli Bunting	X	X	X	
Blue Grouse	X	X		X
Common Raven	X	X		
Northern Pygmy Owl	X	X		
Turkey Vulture	X	X		
Barn Swallow		X	X	
Lesser Goldfinch		X	X	
Western Meadowlark		X	X	
American Crow		X	X	X
Black-billed Magpie		X	X	X
Killdeer		X	X	X
Bank Swallow		X	X	X
Canada Goose		X	X	X
Common Merganser		X	X	X
Belted Kingfisher		X	X	X

TABLE 70 cont.

Bird species	Basin orientation North side (n = 20)	East side (n = 20)	South side (n = 16)	West side (n = 24)
Northern Goshawk		X	X	X
Pacific-slope Flycatcher		X	X	X
Mountain Bluebird		X		X
Ring-billed Gull			X	
Winter Wren			X	X
Swainson's Thrush				X
Frequency ≥ 10%:				
Pine Grosbeak	X		X	X
Spotted Sandpiper	X		X	X
Rufous Hummingbird	X		X	X
White-crowned Sparrow	X	X	X	
Spotted Towhee	X	X		X
Common Nighthawk		X	X	
Sum of absent species	*18*	*9*	*8*	*10*

Concordance Among Diversity Measures

Measures of Alpha Diversity

The main measures of alpha diversity (total richness, richness by habitat group, and richness by frequency class) were all highly positively correlated (Table 71). Taxonomic richness was positively correlated with all other measures of richness. All but one of the pair-wise combinations of measures between habitat associations and frequency classes were positively correlated. The weakest relationships were between upland associates and rare species, and between aquatic-dependents and common species, which were not significantly correlated. Reviewing the species associated with each grouping revealed that all but one of the aquatic-dependent species were rare, and 60% of the riparian–meadow associates were also rare, with only 30% of the upland associates being rare. Conversely, only 30% of the rare species were upland associates, whereas 80% of the common species were upland associates.

Alpha and Beta Diversity

An average of 78.3 (range = 69 to 87, SE = 5.17) bird species were shared among segments (n = 20 reaches per segment), based on segment comparisons across all environmental gradients. The average richness lost or gained between segments was 6.6 species (range = 0 to 17, SE = 0.78), and it was not significantly different (based on paired t-test across gradients, P = 0.795) than the average number of species turnovers between segments ($\bar{x}$ = 6.7 species, range = 3.7 to 10.3, SE = 0.67). The average number of species shared among segments constituted 77.5% of all species observed, and variation in richness and species turnover constituted 6.6% and 6.3%, respectively, of all species observed.

TABLE 71. Correlations among measures of bird alpha diversity. Bolded values indicate $P \leq 0.05$. Shading indicates redundant cells. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Taxonomic richness		Aquatic-dependent richness		Riparian–meadow associate richness		Upland associate richness	
Bird richness measures	r	*P*	r	*P*	r	*P*	r	*P*
Taxonomic richness								
Aqua dependents	**0.482**	**<0.001**						
Riparian–meadow associates	**0.782**	**<0.001**						
Upland associates	**0.848**	**<0.001**						
Rare species	**0.658**	**<0.001**	**0.774**	**<0.001**	**0.709**	**<0.001**	**0.315**	**0.004**
Common species	**0.889**	**<0.001**	0.115	0.171	0.577	**<0.001**	**0.913**	**<0.001**

The analysis of the relative influence of environmental gradients on gamma diversity in the basin showed that the forest to meadow gradient had the greatest contribution to gamma diversity in the basin (Fig. 29). The forest to meadow gradient showed a shift of 39 species along its gradient, almost 40% of the total bird fauna. The forest to meadow gradient was followed by elevation, aspen–cottonwood, and snag and log. Elevation–precipitation gradient would have ranked next to the elevation gradient, with a total change in composition of 37 (alpha = 19, beta = 18). The difference in compositional change among the gradients ranged as high as 21 species—over 20% of the observed total species richness—with all gradients differing by a maximum of 10 species (approximately 10% of the bird fauna).

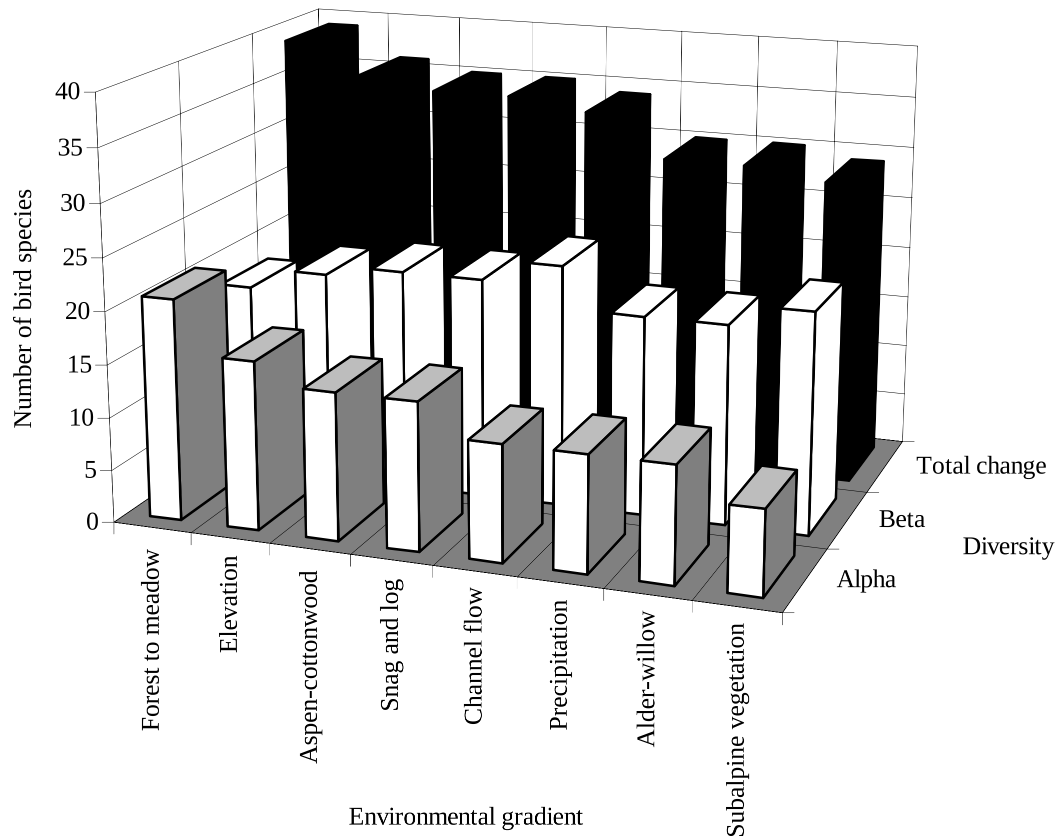

FIG. 29. Contribution of each of 8 environmental gradients to bird diversity of the Lake Tahoe basin. Total change in composition is shown, along with the composite contributions of alpha and beta diversity. Data were collected on 80 sample reaches, 1995 to 1996.

The total change in composition was more closely correlated with alpha diversity (r = 0.919, P = 0.001) than beta diversity (r = -0.103, P = 0.808), and the individual contributions of alpha and beta diversity were not correlated (r = -0.486, P = 0.221). In general, net changes in richness (alpha diversity) along gradients were lower but more variable ($\bar{x}$ = 13.3, SE = 1.41) than changes in composition (beta diversity) ($\bar{x}$ = 20.3, SE = 0.56). Declines in the total change in composition associated with each gradient corresponded with widening differences in the contributions of alpha and beta diversity. Alpha and beta diversity had a similar magnitude of contribution to the total change in composition associated with the forest to meadow gradient, as well as the elevation–precipitation gradient. Changes in composition along the elevation, aspen–cottonwood, and snag and log gradients were more strongly influenced by beta diversity than alpha diversity (Fig. 22).

DISCUSSION

Environmental Influences on Bird Diversity

Despite its small area and high elevation, the Lake Tahoe basin exhibited a high richness of 101 bird species of which a large percentage, almost 40%, were aquatic, riparian, or meadow associates. Although reaches ranged widely in environmental conditions, they shared many species, with any given reach containing an average of 35% and as high as 50% of the species observed throughout the basin. Consequently, turnover was very low, ranging from only 3 to 7% from the lower to upper ends of the 8 environmental gradients examined. Therefore, environmental features that affect alpha diversity (patterns of richness per reach) are the most potent influences on the diversity of birds in the basin.

Alpha diversity was highest at low elevations on low-gradient reaches with meadow vegetation. The negative relationship between bird richness and abundance and elevation was driven primarily by species associated with aquatic, riparian, and meadow environments; however cavity-nesters were also less abundant at higher elevations. Only 1 to 2 aqua-dependent species were observed on reaches over 2200 m, but as many as 7 aqua-dependent species were observed on reaches below 2200 m. Although a total of only 11 aqua-dependent species were detected, they represent a diverse segment of the bird assemblage in the Lake Tahoe basin. Reaches with > 30% meadow exhibited an enhanced level of richness, comprised primarily of riparian–meadow associates. The enhanced level of richness was also observed for aqua-dependent species where canopy cover was < 20%, reflecting a positive association of between aqua-dependent species and meadow.

Among sites that were low elevation and low gradient with meadow vegetation, the occurrence of alder–willow, aspen–cottonwood, and lodgepole pine created a diversity of conditions that supported a greater variety of aqua-dependent, riparian–meadow, and upland species. Aspen–cottonwood and lodgepole pine primarily occurred on mid to low elevation reaches, whereas alder–willow varied in abundance among mid to low elevation sites. All 3 of these vegetation types were positively associated with species richness, but different groups of species were associated with each type. Lodgepole pine and aspen–cottonwood were associated with greater total species richness. However, whereas lodgepole pine was associated with a greater richness of aqua-dependent and riparian–meadow associated species, aspen–cottonwood was associated with a greater richness of common species. Alder–willow was positively correlated with riparian-meadow–associated species. Thus, together these 3 vegetation types supported a diversity of species among mid to low elevation reaches.

Orographic effects on bird species diversity were substantial. The east and south sides of the basin were associated with significantly greater richness than west and north sides. The east side of the basin appeared to provide an ideal combination of lower elevation, drier areas dominated by upland forest vegetation such as mixed conifer, and a relatively abundant amount of aspen–cottonwood, such that it supported a diversity of common, upland species. However, rare species, aqua-dependents, and riparian–meadow associates were most diverse on the south side of the basin, where wide streams and lodgepole pine were most prevalent and alder–willow and canopy cover were lowest. Wide streams were not prevalent among the sample reaches, and it is likely that the open stream environments on the south side, and to a lesser extent on the west side of the basin, were among the few areas with suitable habitat for some species, such as Spotted Sandpiper and Canada Goose.

The contributions of turnover to the diversity of birds in the Lake Tahoe basin were primarily associated with a few gradients, namely channel flow and orientation, with elevation, aspen–cottonwood and snags and logs invoking more minor levels of turnover. Species turnover along the channel flow gradient was driven by opposing relationships between rare and aquatic-dependent species associated with high channel flow and common and upland species associated with low channel flow. The contributions of basin orientation to species turnover reflected a combination range-wide distributional limits and habitat associations. For example, Swainson's Thrush occurs east of the basin into Nevada, so the apparent restriction of this species to cooler, wetter orientations reflects habitat associations versus distributional limits. Similarly, Common Raven, Northern Pygmy Owl, and Turkey Vulture were only found on the warmer, drier orientations in the Lake Tahoe basin, and since they are widely distributed in California and Nevada (Zeiner et al. 1990a, Ryser 1985), their distribution in the basin probably reflects habitat associations. Conversely, the restriction of Winter Wren, Ring-billed Gull, Pine Grosbeak, and Rufous Hummingbird to the west side of the basin may represent the western most extension of their ranges at the latitude of the Lake Tahoe basin, given that they were absent from the east side of the basin and do not occur in Nevada. The apparent differentiation of the bird assemblage between the warm, xeric versus cool, mesic orientations represents a shift in habitat conditions for individual species, but also reflects a larger-scale shift in climate from coastal to continental, which also demarcates the division between 2 major zoogeographic regions (Udvardy 1969, 1975). The low turnover rates observed along the precipitation gradient provide further evidence that shifts in species composition from the west to the east side of the basin primarily reflect shifts in larger-scale distributions, and secondarily reflect the distribution of suitable habitat for individual species.

Although richness was lower at higher elevation reaches, turnover was still observed along the elevation gradient. It is known that some bird species specialize in higher elevation environments (e.g., Zeiner et al. 1990a, Young et al. 1998). I found high elevation affinities in the occurrences of 5 species (e.g., Lazuli Bunting, American Dipper, Common Raven, Blue Grouse, Ruby-crowned Kinglet), while many more species (n = 17), such as American Crow, Canada Goose, Mallard, and Spotted Sandpiper, occurred only in lower elevation environments.

Aspen–cottonwood supported not only a high richness of species, but also a unique assemblage of species. For example, most of the species absent from the lower end of the aspen–cottonwood gradient were granivorous and insectivorous ground foragers (Western Meadowlark, Killdeer, Lesser Goldfinch, Spotted Towhee) or aerial foragers (Barn and Bank Swallow), indicating that aspen–cottonwood stands are a rich source of plant and insect food resources. Also, aspen is a relatively soft wood and provides a suitable nesting substrate for many cavity excavating and nesting birds, as evidenced by the observed association of Northern Pygmy Owl with aspen–cottonwood (DeByle 1985).

Snags and logs provided unique structural and resource conditions that supported a lower overall richness but supported a greater abundance of forest-associated bird species. Associations of a unique assemblage of species along its gradient are evidenced by an intermediate level of turnover relative to other gradients. The decrease in species richness and abundance in association with higher snag and log densities was primarily driven by the richness of aqua-dependent and riparian-meadow associated birds, which are more common in meadow environments (as opposed to forested environments) where snags and logs are naturally less prevalent. While increases in the abundance and turnover of cavity nesters along the snag and log gradient were expected, none were observed.

Individual Species and Species Groups

The investigation of rare species and habitat specialists (i.e., aqua dependents and riparian–meadow associates) greatly enhanced my ability to identify key environmental features that may only be relevant to a subset of species or for which subsets of species had strongly opposing relationships. Essentially, aqua-dependent and riparian–meadow associated species were rare, and upland associated species were common. Therefore, the environmental relationships of rare species were almost identical to those of aqua-dependent and riparian–meadow species. Differing environmental relationships between aqua-dependent and upland-associated species were observed (i.e., opposing relationships with channel width and canopy cover index), but they were masked in assessments of total species richness. Environmental relationships of total bird richness generally reflected those of aqua-dependent and riparian-meadow–associated bird species. Although aqua-dependent and riparian–meadow species generally exhibited similar environmental relationships, riparian-meadow–associated birds were more strongly associated with woody vegetation, specifically positive associations with alder–willow and lodgepole pine.

A number of species exhibited limits in regard to one or more environmental gradients. Although it is likely that many rare species are specialists, a number of factors could be responsible for the observed limits along major environmental gradient, such as suitable habitat being rare, detectability being low, and the Lake Tahoe basin being at the edge of their range. However, 7 species were detected at $\geq$ 10% of the reaches and were restricted in their occurrence along one or more gradients suggesting specific bounds in the extent of their niches in the basin: Spotted Sandpiper, Mallard, Spotted Towhee, Tree Swallow, American Dipper, White-crowned Sparrow, and Black-headed Grosbeak. These species, although frequently occurring, may be particularly susceptible to environmental changes, and should be considered specifically in riparian management.

Most of the species restricted to certain segments of the major environmental gradients were absent from upper elevation environments, including Tree swallow, Spotted Towhee, Black-headed Grosbeak, and Mallard. These species differ greatly in their foraging substrates and foraging behaviors, but they are all insectivorous to some degree. Spotted Sandpipers were absent from the highest elevation reaches, but also from highest gradient reaches and the east-side of the basin where channel flow was generally low. The Spotted Sandpiper is a ground nesting bird that forages, in part, by wading in water and capturing insects from the bottom of the stream (Zeiner et al. 1990a). Channel flow may be a limiting habitat feature for the Spotted Sandpiper, which may not find suitable foraging and nesting conditions in association with narrow, high gradient reaches at higher elevations. In contrast with these lower elevation associates, American Dipper was associated with higher elevation and precipitation. The American Dipper is an aqua-dependent bird that forages underwater for invertebrates and fish (Zeiner et al. 1990a). It is commonly associated with fast-flowing streams and high elevations during the breeding season.

Uniquely, White-crowned Sparrow was absent from reaches with higher densities of snags and logs. The White-crowned Sparrow is a riparian associate and a ground foraging granivore, most often foraging in open grassy habitats (Zeiner et al. 1990a). The restriction of the frequently occurring White-crowned Sparrow to reaches with low densities of snags and logs is probably more directly a function of abundance of meadow which was negatively correlated with snags and logs.

Conservation and Management Implications

It is clear that riparian environments support a greater richness of bird species than upland environments in the Sierra, and that the Lake Tahoe basin supports a high diversity for its elevation. Studies in riparian environments at varied elevations in California, Oregon, and Colorado detected totals of 64, 116, and 124 bird species, respectively (Knopf 1985, Lynn et al. 1998, Sanders and Edge 1998). In contrast, studies in non-riparian habitats in the Sierra Nevada detected only about 50 bird species (Hejl et al. 1988, Verner and Larson 1989). Vegetation had the greatest influence on bird species richness and abundance in the Lake Tahoe basin, whereas channel flow and elevation factors had the greatest influence on species composition. The diversity of vegetation types at low to mid elevations, namely meadow, lodgepole pine, alder–willow, and aspen–cottonwood, is largely responsible for the relatively high species richness observed in the basin compared to similar environments studied by others. The steep elevation, precipitation, geomophological, and orographic gradients also create a diversity of environments. Additionally, the Lake Tahoe basin also lies along a major east–west division between biogeographic zones providing an enhanced assemblage of species. The combination of these varied conditions is the key progenitor of high bird diversity in the riparian areas in the basin.

The majority of birds found riparian environments to be suitable throughout a large proportion of the Lake Tahoe basin, as evidenced by high alpha diversity. High richness per site suggests that conservation strategies for birds could have a great deal of flexibility to accommodate other conservation or development considerations. The identification of areas with the highest diversity of bird species, particularly less common species, would be an important step. However, once identified, the location of additional sites with an emphasis on maintaining and conserving biological diversity could be flexible. The applicability of a combination coarse- and fine-filter approach (Noss and Cooperrider 1994) for the purposes of conserving bird diversity in the Lake Tahoe basin is discussed below.

The proportion of species considered rare was not particularly high relative to other studies, although absolute comparisons of rarity were often not possible since most studies used different measures of rarity. Goerck (1997) and Kattan (1992) found that approximately 30% of all bird species were present at only a few sample sites in the forests of Brazil and Columbia, respectively. In forested environments of the Sierra Nevada, Verner and Larson (1989) found over 40% of all birds were present on less than 10% of the sites sampled, whereas Hejl et al. (1988) found only about 10% of the birds detected on less than 10% of their sample sites. Reed (1995) determined that almost 70% of all birds in the Great Basin were "uncommon". These comparisons are coarse, not only due to the varied measures of rarity, but also because sampling intensity varied among studies. Nonetheless, they illustrate that the proportion of a given bird assemblage considered rare or uncommon can range from 10% to almost 70% of the species, depending on the geographic location, sampling, and criteria applied.

Bird species richness is often negatively associated with elevation (e.g., Able and Noon 1976, Knopf 1985, Rahbek 1997, Young et al. 1998). For example, high elevation coniferous forests commonly support fewer species of vertebrates than lower elevation vegetation type in the Sierra as a result of shorter growing seasons, lower primary productivity, higher moisture stress, and lower production of insects and other invertebrates that provide basic food resources for many species (Verner and Purcell 1988). Overall, food availability in aquatic environments would also be reduced at higher elevations because productivity generally declines with stream order and temperature (Sheldon 1968, Vannote et al. 1980, Allan 1995). Higher species richness at low elevations combined with unique species occurring at higher elevations could make for a demanding conservation scenario. However, threats to environmental conditions in high elevation areas in the Lake Tahoe basin are generally limited to fire management and non-motorized recreation. Lower elevation environments are most vulnerable to human disturbance in the basin. Threats to lower elevation sites will vary depending on the type of environment (e.g., meadow, mixed conifer forest). A conservation strategy for the biological diversity of birds would be most effective if efforts were concentrated at lower elevation sites and encompassed as broad a diversity of vegetation types and aquatic environments as possible, since gains in bird diversity will be incremental and will generally track the diversity of environments.

The management of meadows, particularly those at mid to low elevations, could have significant effects on the richness of aquatic, riparian, and meadow associated birds. Thresholds observed for bird species richness in relation to the amount of meadow and associated canopy cover corroborate the results of other studies showing that resources associated with meadows (e.g., food, cover, nest sites) may reach necessary levels of abundance or diversity only in meadows above a certain size or extent (e.g., Bowers 1986, Linusson et al. 1998, Wettstein and Schmid 1999). The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows (Ratliff 1985). Agencies within the Lake Tahoe basin are increasing the use of prescribed fire in an attempt to restore the function of fire in reducing flammable fuels. Prescribed fires and wildfires that are allowed to burn should generally improve the quality and quantity of meadows in the basin. Water diversions are rare in the basin, but channel restoration efforts are relatively common (TRPA 1997), and future efforts should consider potential impacts on meadow systems. Most meadows in the basin are currently grazed by cattle, and few allotments exclude cattle from grazing adjacent to stream channels (USDA 1988). Grazing can have a deleterious effect on many bird species, particularly ground and shrub nesting aquatic, riparian, and meadow associated species (e.g., Bock et al. 1992).

Lodgepole pine stands, particularly in association with meadows, played an important role in supporting high species richness at lower elevations. Lodgepole pine stands tended to be open-canopied, and in some instances they were so sparsely forested that they may have functioned more as a savanna grassland than a forested stand. Adjacent to streams, as in this study, the understory of lodgepole pine typically consists of grasses, forbs, and sedges (Bartolome 1988, Potter 1994). It is commonly considered to have low value to birds and other vertebrates in the Sierra Nevada because of its low vertical diversity (Verner and Boss 1980). However, the fact that reaches with lodgepole pine consistently supported at least 6 species of riparian–meadow associates contradicts the notion that lodgepole pine near streams has low value for bird species. Any effort to conserve the richness and diversity of aquatic, riparian, and meadow bird species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine in proximity to streams and meadows. Potential management impacts include cattle grazing and fire management.

Alder–willow provided valuable habitat for riparian-meadow–associated bird species, as well as supporting common species. Alder and willow are often noted as having high species richness and abundance (e.g., Morrison et al. 1994, Lynn et al. 1998, Warkentin and Reed 1999), and it is to be expected that riparian-associated species would be more speciose (and abundant) in riparian-associated vegetation. However the negative association of rare and aqua-dependent species with alder–willow indicates that alder–willow can potentially degrade the suitability of a stream reach for some aqua-dependent species. Alder–willow may pose a physical barrier to foraging by aqua-dependent species, as well as potentially reducing stream productivity by occluding sunlight. Conservation efforts should not assume that more alder–willow will necessarily enhance the diversity of stream-associated bird species.

Alder and willow occurred frequently along stream reaches, and was generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, however grazing and channel restoration could alter its abundance. Species such as the Willow Flycatcher (*Empidonax traillii*) are dependent upon willow as a nesting substrate. The abundance and condition of willow appear to affect its site selection, and grazing cattle can affect its nest success both directly, through physical disturbance, and indirectly, through nest parasitism by the Brown-headed Cowbird (Brown 1994, Fleischner 1994, Uyehara and Narins 1995, Johnson et al. 1999). Channel restoration could affect alder and willow abundance, as well as meadow conditions. Restoration efforts that involve key meadow complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow bird habitat.

Aspen–cottonwood had a strong influence on bird diversity through a combined influence on richness and turnover. Aspen communities are considered highly productive environments because of their high insect populations and the high food value associated with their catkins, buds, and leaves (Brinkman and Roe 1975, Verner 1988), and have been found to be associated with bird species richness and abundance in other studies (e.g., Szaro 1977, Anderson et al. 1983, Strong and Bock 1990). The fact that it rated relatively high in diversity (richness and composition) in spite of occurring infrequently on sample reaches suggests that aspen and cottonwood may function as keystone species (e.g., Daily et al. 1993, Power et al. 1996) relative to bird diversity in the Lake Tahoe basin. A keystone species is one "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power et al. 1996). Daily et al. (1993) suggest that aspen in subalpine ecosystems of Colorado functions as part of a keystone complex along with sapsuckers, which excavate cavities and drill sap wells which in turn provide resources for many other vertebrate and invertebrate species. It is likely that such a complex of interactions is also occurring in the Lake Tahoe basin where sapsuckers, as well as many other cavity nester, occur in aspen and cottonwood stands.

Given the substantial contribution of aspen and cottonwood to bird diversity in the Lake Tahoe basin, it would be ideal to manage aspen for its wildlife values. Larger stands of aspen and cottonwood may provide particularly valuable habitat for a wide array of species, given that other studies have found that stand size can significantly effect the richness and abundance of associated birds (e.g., Johns 1993). Aspen stands are sometimes ephemeral vegetation associations which are succeeded by conifer forests in the absence of fire. However, depending on soils and moisture, some aspen stands can be relatively permanent features even in the absence of fire (Barry 1971, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

A high density of small snags and logs occur in the Lake Tahoe basin as a result of recent large-scale tree mortality events (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), as evidenced by the high frequency of occurrence (> 80%) of large snags and both sizes of logs across all sample reaches. Existing stands of dense, small diameter snags and logs appeared to have low suitability for some riparian-associated bird species. In addition, a high abundance of small diameter snags and logs may decrease the suitability of forested environments for some cavity nesters. Snags must be a minimum diameter to provide nesting habitat for cavity-nesting birds (with larger-bodied birds requiring larger diameter snags), and smaller logs provide more limited foraging opportunities (Maser et al. 1979). Management of snags and logs to benefit bird diversity should focus on the retention and recruitment of large snags and logs. Attempts to reduce fine fuels in the Lake Tahoe basin may reduce the density of small snags and logs, but may also pose a risk to the quality and quantity of large snags and logs. Large snags can pose a safety hazard during burns, and charring can reduce the suitability of snags and logs for wildlife species. Careful fire management to conserve values provided by large snags and logs would contribute to retaining valuable habitat elements for many bird species.

High channel flow was associated with a greater richness of aquatic, riparian, and meadow associated bird species. Similar patterns of richness were found by Lynn et al. (1998) in the nearby Truckee River, where riparian bird species richness was higher at lower stream reaches. They asserted that reductions in the width and amount of riparian vegetation, combined with higher elevations, were probably responsible for lower richness on upper watershed stream reaches. Rivers are traditionally viewed as a longitudinal gradient, where high-gradient upland streams with small channels, cold temperatures and highly oxygenated water transition into low-gradient channels with a diversity of channel forms, large floodplains, and more regular, predictable abiotic conditions that, all together, result in a shift in the type and range of habitats, food sources, and biotic diversity from headwaters to mouth (Petts and Calow 1996). Additionally, shifts in the trophic structure of streams from headwaters to mouth have been proposed as a general pattern that can be found in most streams (i.e., the "river continuum concept"; Vannote et al. 1980). Undoubtedly, geomorphological shifts along the channel and associated shifts in aquatic and riparian biota would affect many of the bird species I detected, such as American Dipper, Belted Kingfisher, Osprey, and Spotted Sandpiper which forage exclusively on aquatic and aquatic-associated biota (Ehrlich et al. 1988). As mentioned above, channel restoration efforts in the Lake Tahoe basin are relatively common, and could potentially degrade bird diversity if not designed with bird diversity as one of the objectives.

The conservation of specialists, rare species, orographically or environmentally restricted species is a critical element of any effort to conserve biological diversity. Patterns of richness and turnover provide valuable insights into environmental features that support the majority of species. The concept of a coarse-filter approach to conservation, developed by the Nature Conservancy (Noss 1987), would apply well in the case of conserving the majority of stream-associated bird species in the Lake Tahoe basin. The coarse-filter approach would entail conserving a breadth of vegetation and aquatic community types without specific attention paid to the species associated with each. Fine-filter conservation approaches complement coarse-filter approaches by considering additional environmental requirements for species that are not supported by a coarse-filter approach (Noss and Cooperrider 1994). Fine-filter approaches focus on species that are specialists, rare, geographically restricted, or declining in numbers (Noss and Cooperrider 1994). The individual species identified as potential specialists, as well as species considered rare or limited to 1 to 2 basin orientations, are good candidates for individual conservation considerations. For example, certain orientations may offer the only suitable habitat for some species of birds. The location, distribution, and timing of conservation actions (e.g., water development projects, control of exotics) and management treatments (e.g., prescribed fire, timber harvest, road building) should take into consideration the potential impacts on geographically limited species. Species known to be declining in numbers were not specifically addressed in this study, but obviously they should also be included in the development of any fine-filter conservation approach.